Will Davies, 11.5.25

Cortical Colour for Philosophers: The Demise of Opponent-Process Theory

Few scientific ideas have shaped philosophical theories of colour experience as much as opponent-process theory (OPT). Its influence, cemented by Hardin's (1988) seminal *Colour for Philosophers*, lies in its promise of aligning perceptual phenomenology with underlying neural processes. OPT offers an attractively simple picture: colour experience arises from fixed neural channels for the opponent pairs of red-green (RG) and yellow-blue (YB), and the nonopponent duo of white-black (WBl). Block (2023: 52) captures the current mood:

> the opponent process theory… was discovered in the nineteenth century by Ewald Hering and further elaborated by Dorothea Jameson and Leo Hurvich in the 1950s... Then the theory was validated by finding opponent cells in the lateral geniculate nucleus and later refined using both neural and behavioural data.

The words 'discovered,' 'validated,' and 'refined' suggest that OPT provides a secure neuroscientific foundation for debates about colour experience. Many philosophers have taken this for granted.[1]

Recent neuroscience calls this foundation into question. Studies of primary visual cortex (V1), the first cortical site for chromatic signal integration, reveal complexity where simplicity was predicted. V1 does not transform the broadband channels of LGN into new canonical streams, rotated towards RG, YB, and WBl. Instead, V1 exhibits a heterogeneous range of chromatic response profiles, many complex and nonlinear, resisting the bipolar structure posited by OPT. Chromatic signals are integrated with achromatic and spatial-objectual features, yielding mixed selectivity and form-dependence, rather than pure and fixed colour pathways. These findings indicate that much of our philosophical understanding of colour experience rests on an outdated physiological model.[2]

This matters because OPT sustains assumptions that have long influenced philosophical theory. Since antiquity, colour variation has often been explained by

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[1] Examples include Clark (2000: 10-16), Tye (2000: 160-165), McLaughlin (2002: 129-131), Byrne & Hilbert (2003: 13-15), Matthen (2005: 154-157), Pautz (2006: 208-211), Churchland (2007: 133-137; 2012: 50-61), Cohen (2009: 83, 87-88), Papineau (2015: 284-285), Gert (2017: 3-4), and Sharp (2024: 782, 789-790). Hardin (2014) gives an updated take on OPT, though still favourable. Allen (2016: 70, 120, 146) and Chirimuuta (2017: 59-63, 123-127) are more sceptical, and Block (2023: 70-71) qualifies his endorsement somewhat.

[2] Related critiques include MacLeod (2010), Brogaard & Gatzia (2017: 137-140), Conway et al. (2023), and Gegenfurtner (2025).

combination of a few basic elements. For Parmenides, Empedocles, and Aristotle, colours arise from proportions of light and dark; later, Renaissance writers like Alberti and da Vinci enumerated a small set of basic colours—typically adding red, yellow, blue, and sometimes green, alongside light and dark—from which the painter's gamut could be produced.[3] On the perceptual side, the natural corollary has been to posit fundamental vehicles whose combinations yield the full range of colour experience. In early modern discussions this often took the form of elementary sensations distributed over a two-dimensional array: a pointillist 'sensory core' from which object perception is built.[4] The nineteenth century added physiological backbone. On Young (1802) and Helmholtz's (1876) trichromatic theory, the basic sensations are three—roughly red, green, and blue—tied to distinct cone classes, now understood as L, M, and S rather than R, G, and B.[5] In Hering's competing account, the primitives RG, YB, and WBl are linked to opponent physiological processes; in this spirit Mach (1959: 67) describes the 'fundamental sensations white, black, red, yellow, green, blue, and six different corresponding (chemical) processes… in the retina.'[6]

Contemporary OPT reframes this 'primitives' impulse in representational terms: basic sensations give way to functionally independent channels that encode coordinate values along fixed RG, YB, and WBl axes. This invites philosophical assumptions about format, on which the vehicles of colour representation have an axis-coordinate structure, factorised chromatic and achromatic components, and no sensitivity to spatial-objectual form at the point of encoding. The evidence against OPT calls these assumptions into question, forcing a significant philosophical reorientation.

Here is the plan. Section 1 describes OPT, highlighting its predictions for early cortical processing, and connecting these with philosophical assumptions about representational format. Section 2 argues that OPT's predictions are not borne out in V1, and explains what is found instead. Section 3 concludes by discussing the implications for colour representation, and outlines the required reorientation.

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[3] For discussion, see Kuehni & Schwartz (2008: 31-32, 37-38, 330).

[4] This idea originates with Descartes's (1637/1985) 'second grade' of sensation, which comprised the mind's imprint of the retinal (strictly, pineal) image; see Hatfield & Epstein (1979) and Hatfield (1990).

[5] This is an instance of Müller's (1838/1842) *Law of Specific Nerve Energies*, discussed by Isaac (2019).

[6] Brentano (2009: 127–160) held that an experience of purple is composed by imperceptibly small blue and red parts, though these parts were conceived as primitive intentional objects rather than sensations. For discussion, see Massin & Hämmerli (2017).

1. *What is Opponent-Process Theory?*

We must first distinguish OPT from *opponent-colour theory* (OCT). OCT is a phenomenological account of the structure of colour experience, originating with Hering (1905/1964). OCT claims, first, that every experienced colour can be characterised by proportions of four chromatic primaries (R, G, Y, B) and two achromatic primaries (W, Bl). Second, the chromatic primaries bear opponent relations, with no experienced colour characterizable as both R and G or Y and B. Third, the achromatic primaries are contrary but nonopponent, as experienced greys are characterizable as both W and Bl. Fourth, some experienced colours are *unique*, characterizable by just one primary, such as a red that seems to contain no proportion of Y, B, W, or Bl. OCT thus implies a 3D phenomenological colour space, structured by the contrary pairs RG, YB, and WBl, as in the Natural Colour System.[7]

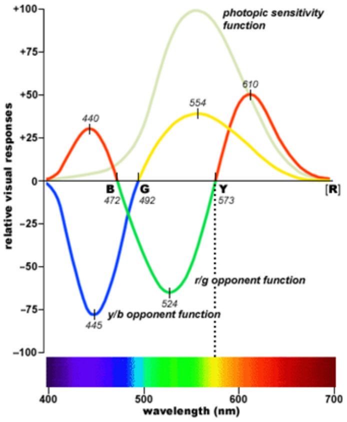

Figure X. Hue scaling curves based on data from [Hurvich & Jameson (1957)].

OCT was refined by Hurvich and Jameson's (1957) seminal hue-cancellation experiments. Implicit in OCT is the idea that a light that appears R can be made to appear neither R nor G by adding some proportion of G light to it. The experiments thus quantified the relative R response produced by a stimulus by measuring the amount of G light required to 'neutralise' it—mutatis mutandis for G, Y, and B. Responses were plotted against wavelength to yield a *hue scaling curve* for each primary. These curves are spectrally broadband, spanning on the order of 100nm, together tiling the entire visible spectrum (~400-700nm). Whereas the R curve overlaps Y and B, it does not overlap G, reflecting RG opponency. By convention, R and G—likewise, Y and B—are combined into a continuous bipolar *opponent scaling curve* with a positive R (Y) and negative G (B) lobe (Figure X). The

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[7] For discussion of the NCS, see Hardin (1988: 116-121), Hård et al. (1996), Sivik (1997), Kuehni & Schwarz (2008: 100-113), Allen (2016: 88, 121-128, 142-146), and Matthen (2020: 164-166).

curve crosses zero where R and G are balanced, with responses characterised solely by Y or B, corresponding to a unique yellow or blue. By comparison, scaling achromatic responses yields a unipolar curve resembling the photopic luminosity function, peaking around 560nm.

OPT offers a constitutive explanation of OCT in terms of neural-cum-computational mechanisms—that is, mechanisms composed of neural parts, which implement certain computational processes.[8,9] As will become clear, computational- and algorithmic-level descriptions are thus integral to OPT's mechanistic explanation. The core hypothesis is that colour experience is produced by activity in a small set of *opponent appearance mechanisms* (OAMs), which map cone excitations to coordinates within a perceptual colour space structured by RG, YB, and WBl. The standard version posits one OAM per pair: effectively, each OAM delivers coordinates along one axis—RG, YB, or WBl—within a 3D opponent frame. Idealising, the RG OAM, for instance, outputs values 1 and –1 for unique R and G, and 0 when R and G are balanced. It is thus selectively excited by R and inhibited by G, showing physiological opponency. Its spectral response function—output plotted against wavelength—should be isomorphic to the RG opponent scaling curve: broadband in nature, with zero-crossings at unique yellow and blue.

Hardin (1988: 34-35) popularised a canonical *two-stage OPT*, on which cone signals are linearly combined along three *cone-opponent channels*—L–M, S–(L+M), L+M—identified with RG, YB, and WBl OAMs, respectively.[10] Key evidence for this model came from electrophysiological studies of lateral geniculate nucleus (LGN) and psychophysical detection tasks. Derrington, Krauskopf, and Lennie (1984) provided systematic mappings between LGN cells and retinal cone activity in macaques. Stimuli were modulated along various directions in the eponymous DKL colour space, which has axes corresponding to the hypothesised channels (Figure Xa). On the horizontal, 0° and 180° represent positive and negative activity in L–M; 90° and 270° likewise for S–(L+M). On the vertical, +/-90° represent positive and negative activity in L+M. The main finding was that almost all LGN cells were tuned to these so-called *cardinal directions*. As Figure Xb shows, the majority of chromatically selective cells gave peak responses near 0° or 180° hue, with the remainder

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[8] Craver (2007) provides a seminal account of constitutive mechanistic explanation.

[9] OPT clearly would be undercut, if OCT were found to be deficient. While outside the present scope, Conway et al. (2023) offer a provocative critique; see also Jameson & D'Andrade (1997), Bosten & Boehm (2014), Wool et al. (2015), and Witzel et al. (2019).

[10] The model follows Boynton (1979). Alternatives were proposed by Hurvich & Jameson (1959: 388), Guth & Lodge (1973), and Ingling & Tsou (1977). Note that the labels 'L–M' etc., only convey the identity and sign of the predominant cone inputs to each mechanism, not their relative weights.

clustered around 90° and 270°. The cells thus formed two fairly discrete populations, with chromatic preferences aligned with the L–M and S–(L+M) axes.[11]

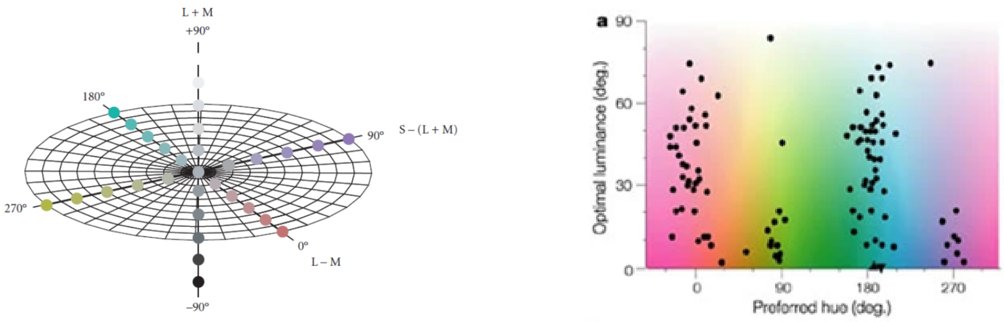

Figure X. (a) DKL colour space [Stockman & Brainard (2010)], (b) Chromatic tuning of LGN cells [Gegenfurtner (2003)].

In psychophysics, Krauskopf and colleagues (1982) examined how contrast adaptation affected chromatic detection thresholds. They first established subjects' thresholds along various directions in DKL space. Subjects were then adapted to drifting gratings of low spatial frequency (SF), modulated along cardinal or noncardinal directions (45°/225° or 135°/315°). When thresholds were retested, the effects of adaptation were highly direction-selective. Adapting to modulations along 0°/180° raised thresholds for contrasts along the L–M axis, but not S–(L+M). Similarly, modulations along 90°/270° raised thresholds along the S–(L+M) axis, but not L–M. In contrast, modulations along noncardinal directions produced broader elevations in thresholds, showing little direction-selectivity. This supports the existence of chromatic detection mechanisms aligned close to the L–M and S–(L+M) axes, but not intermediate axes.[12]

As De Valois and De Valois (1993: 1053) note, by the 1980s two-stage OPT was 'the accepted dogma in colour vision, the Standard Model.' Yet significant failings were evident as early as the 1950s.[13] First, the response functions of L–M and S–(L+M) cells are not isomorphic with the RG and YB scaling curves.[14] Jameson and Hurvich (1957) found that the RG curve included a small positive lobe below 470nm, reflecting the fact that purples appear as mixtures of blue and red. Because excitation in this region involves S-cones, it was

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[11] For further evidence, see Shapley & Hawken (1999), De Valois et al. (2000), Reid & Shapley (2002), and Cooper et al. (2012). On the retinal origins of cone-opponent channels, see Lee et al. (1998), Dacey (2000), and Martin et al. (2001), though Godat et al. (2024) suggests more diverse retinal encoding than previously reported.

[12] Guth & Lodge (1973), Ingling & Tsou (1977), and Thornton & Pugh (1983) suggested something similar.

[13] Jacobs (2014) discusses some of the relevant history. Hardin (1988: 38, 127) noted some limitations, but this did not stop the model gaining philosophical currency.

[14] See Abramov & Gordon (1994: 468), De Valois et al. (1997), Mollon & Jordan (1997: 382), Mollon (2006: 304), and MacLeod (2010 §6.2). In philosophy, see Broackes (2011: 603), Matthen (2020: 169), and Byrne & Hilbert (2020: 129).

apparent that an RG mechanism must have S-cone input, and that a pure L–M channel would not suffice.[15] Similarly, De Valois and colleagues (1966: 977) observed a poor fit between their putative '+B' and '–B' units—later identified as S–(L+M) cells—and the YB scaling curve. Derrington and colleagues (1984: 264) concurred that these cells' chromatic tuning is 'clearly different from the "unique yellow-unique blue" direction most associated with the activity of the [YB] opponent mechanism.' Psychophysical work has since confirmed that observers' unique-hue settings do not align with the cardinal directions, which are closer to cherry-teal and chartreuse-violet than RG and YB (Figure X).

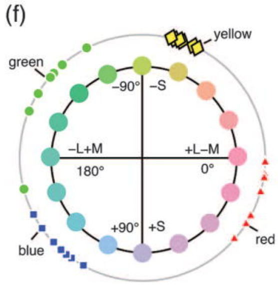

Figure X. Unique hue settings plotted against DKL axes. [Shevell & Martin (2017), using data from Wool et al. (2015).]

Second, the two-stage model assigns achromatic signals to the L+M channel, with L–M and S– (L+M) carrying purely chromatic information. This fit the prevailing physiological view—typified by Livingstone and Hubel (1987)—that achromatic signals are confined to the magnocellular pathway, where most units sum L- and M-cone inputs. Yet Derrington and colleagues (1984) found that parvo LGN cells typically preferred combined chromatic-luminance contrasts. As Figure 1b shows, cells tuned near 0° and 180° hue spanned almost the full vertical axis, from 0° (pure chromatic selectivity) to 90° (pure luminance selectivity). Their optimal stimuli ranged accordingly from saturated cherry-reds to bright, desaturated cherry-reds. Cells tuned near the S–(L+M) axis—thus primarily koniocellular—showed less luminance selectivity, clustering between 0-20°.[16] De Valois and De Valois (1993: 1061) conclude that 'much if not most of the achromatic information involved in vision comes up the… parvo pathway, multiplexed with the chromatic information.'[17]

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[15] Derrington and colleagues (1984: 252-253) found that the L–M cells in LGN received almost zero S-cone input, meaning that any combination must come later. For discussion, see Shevell & Martin (2017: 1103).

[16] No L-M or S-(L+M) cells preferred negative luminance changes, towards darkened hues. For discussion, see Gegenfurtner (2003: 565-566) and Shevell & Martin (2017: 1105). On S-cone signals and the koniocellular pathway, see Hendry & Yoshioka (1994) and Hendry & Reid (2000).

[17] Stockman & Brainard (2010: 38-39; 49-50; 76-79) discuss multiple possible luminance pathways. Creutzfeld et al. (1986) argue that parvo LGN cells code chromatic and brightness contrast; cf. Koenderink et al. (2018).

Third, this is symptomatic of a deeper problem. On the canonical two-stage account, cone-opponent channels implement a context-invariant mapping from LMS excitations to postreceptoral coordinates (L–M, S–(L+M), L+M), which are read out in a fixed (RG, YB, WBl) frame. This model is *form-blind*: it has no parameters for orientation, SF, temporal frequency, or other object-related factors. In practice, though, LGN receptive fields (RFs) exhibit marked spatiotemporal dependence. The very same nominal L–M unit can show high chromatic selectivity for coarse spatial and slow temporal structure, yet high luminance selectivity for finer spatial and faster temporal structure.[18] That is, the effective readout of the L–M signal—the direction that is actually tracked by a decoder of the unit in a given context—rotates towards the achromatic axis under some stimulus regimes. This shows that L–M values cannot be projected onto a fixed perceptual axis: if L–M is the basis, the effective axis rotates with context.

To address these shortcomings, OPT was expanded to include a third cortical stage. To be clear, it was always assumed that OAMs would be cortical rather than geniculate: LGN cells do not adapt in ways consistent with the changes in detection thresholds,[19] and few cells receive S-cone input, with those that do showing weak and sluggish responses compared to parvo L–M cells. As De Valois and colleagues (1966: 977) observed early on, a robust YB mechanism therefore would require S-cone signals to be 'amplified… at some cortical level.' What changed in the 1990s was the recognition that the signals inherited from LGN could not be treated as ready-made carriers of RG and YB content, but would require substantial cortical transformation if OPT was to be preserved.

On De Valois and De Valois's (1993) influential third-stage model, L/M- and S-cone-opponent signals are recombined to form four new chromatic channels,[20]

Red: (L–M) + (S–(L+M))	**Yellow**: (L–M) + ((L+M)–S)
Green: (M–L) + ((L+M)–S)	**Blue**: (M–L) + (S–(L+M))

Here 'L–M' and 'M–L' denote opposite polarities of the same cone-opponent dimension: in the former, L-cones excite and M-cones inhibit; in the latter, the reverse. Likewise, for 'S–

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[18] See Reid & Shapley (1992, 2002) and Lankheet et al. (1998a,b). Johnson et al. (2001) and Hass & Horwitz (2013) discuss RF variability in connection to V1 coding.

[19] See Derrington et al. (1984: 264) and Webster & Mollon (1994: 2014) for discussion.

[20] These channels reflect half-wave rectification of bipolar LGN signals, where the negative response is 'clipped,' yielding a purely positive function. For details, see De Valois & De Valois (1993: 1059-1060) and Stockman & Brainard (2010: 82-84), who also discuss Guth's (1991) alternative third-stage model.

(L+M)' and '(L+M)–S.'[21] In this schematic idealisation, each pair of polarities provides complementary inputs, so that the R and G (likewise Y and B) mechanisms define opposing poles of a new axis, connecting the unique hues about a neutral point. De Valois and De Valois (1993) describe this as 'rotating' the cardinal axes, yielding a new coordinate frame in which the unique hues define the canonical directions.[22] Achromatic information is decoupled from cone-opponent signals by summing their responses,

White: (L–M) + (M–L) + (S–(L+M))

As De Valois and De Valois (1993: 1054) note, LGN neurons can be modelled as having two effective RF structures—one engaged by chromatic stimuli, another by achromatic. Accordingly, a single cell can have different spatiotemporal tuning properties for each stimulus type. Their solution is to pool the effective achromatic RFs of multiple neurons through summation, producing a dedicated achromatic channel.[23]

While this model is strictly neutral about cortical locus, V1 is a crucial testbed. First, the proposed mechanisms recombine LGN outputs, and the overwhelming majority of LGN fibres terminate in V1.[24] It is therefore reasonable to expect third-stage transformations to be implemented in V1, either fully or in part. Second, as Nunez and colleagues (2018: 2) note, 'V1 is a bottleneck for colour perception in the cortex; colour processes occurring later in the cortex are based on the responses from the neural substrates for colour perception in V1.' Even if OAMs are ultimately located downstream, V1 should at minimum deliver signals that are readily transformable into the format OPT requires.[25]

The model thus makes testable predictions about early-cortical coding, with V1 the natural first site to examine. If third-stage transformations are fully implemented in V1, we should observe:

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[21] This reflects the varied RFs of LGN cells: roughly half 'L–M' cells receive excitatory L- and inhibitory M-cone input, the rest vice versa. In contrast, almost all 'S–(L+M)' cells receive excitatory S-cone input.

[22] De Valois and De Valois's (1993, 2000) mechanisms do not actually behave like true opponent axes. Due to half-wave rectification, LGN's bipolar mechanisms are split into four unipolar channels, each with a positive-valued function. The result is that R and G, for instance, do not form exact mirror-image poles of a single axis, but partially overlapping functions that can be co-active at some hue angles. There are no strict neutral points—hence no strictly pure R, G, Y, or B—as defined by the zero-crossings of bipolar response functions.
Their model preserves a vector-summation picture, in which colour is coded by four overlapping basis functions, rather than strict axis-based opponency—thus already a significant departure from a canonical OPT.

[23] Lennie & D'Zmura (1988) offer a similar account. I omit details of the black channel, which involves cells with inhibitory inputs to their receptive field centres, as described by De Valois & De Valois (1993: 1057-1059).

[24] While some studies have reported LGN projections to prestriate cortex, including V2, (Fries, 1981; Yukie & Iwai, 1981; Bullier & Kennedy, 1983), the dominant pathway is to V1.

[25] MacLeod (2010: 160-161) makes a similar point.

I. **Broadband Basis Mechanisms:** V1 recombines LGN signals to form a small set of spectrally broadband chromatic mechanisms aligned with R, G, Y, and B, which give graded responses across a wide range of hues, providing basis signals for later chromatic processes.

II. **Achromatic Segregation**: V1 decouples achromatic signals from cone-opponent signals, forming a functionally independent achromatic pathway.

III. **Spatial-Objectual Invariance**: V1 neurons encode chromatic information in ways that are insensitive to spatial-objectual features such as orientation, spatial frequency, and contour structure.

On a more cautious reading, even partial third-stage transformations should yield broadband mechanisms in V1, with LGN signals remixed into streams that partly rotate the cardinal axes toward RG and YB. V1 should also show increased achromatic segregation, if not a fully independent achromatic pathway, and greater invariance across spatial-objectual features, if not complete stability. Even thus weakened, these are distinctive and falsifiable claims.

In preview, empirical studies challenge each prediction: (i) contra Broadband Basis Mechanisms, V1 houses a heterogenous array of chromatic mechanisms that span colour space, with diverse and often narrowband, nonlinear tuning profiles, rather than broad, axis-like shapes; (ii) against Achromatic Segregation, V1 enhances and functionally exploits mixed chromatic-luminance selectivity, rather than diminishing it; (iii) contra Spatial-Objectual Invariance, most chromatic responses are jointly selective for spatial-objectual features, indicating substantial form-indexing and context-dependence, rather than a form-blind colour code. V1 thus fails to display the signatures envisaged by OPT: instead, we find a picture at once more complex—and more fascinating—than previously imagined.

These findings matter philosophically because OPT underwrites assumptions about representational format that have a strong—if often implicit—hold on philosophical thinking. Beyond the familiar discursive/iconic distinction, OPT invites a more specific assumption: colour is represented in an *axis-coordinate format* marked by *achromatic independence* and *form-blindness*. On this picture, colour contents specify locations in a space structured by RG, YB, and WBl axes.[26] If Broadband Basis Mechanisms obtain, then the representational

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[26] Byrne & Hilbert (2003) propose that contents attribute magnitudes of RG/YB fundamentals—*hue magnitudes*—though this is not the only way contents might specify locations in RG/YB space. For example, a content could attribute *orange* in an unstructured way, yet have accuracy conditions determined by extrinsic relations—such as subjects' dispositions to judge similarities between orange, red, and yellow—that mirror the geometry of RG/YB space. For related discussion, see Allen (2016: 118ff) and Pautz (2020).

vehicles themselves have a corresponding three-part structure, with components that encode coordinates along these axes. Achromatic Segregation further supports a factorised structure: the WBl component varies independently of RG/YB, mirroring the orthogonal achromatic and chromatic axes. Finally, Spatial-Objectual Invariance renders these vehicles form-blind: these components specify coordinates in a context-invariant frame, with axes and metric independent of spatiotemporal or object-related factors. As noted earlier, these assumptions are representational heirs to older 'elemental vehicles' views: where once there were primitive, pre-objectual R/G/B sensations, now there are basic, object-independent representations for RG/YB/WBl. The empirical evidence reviewed below undermines OPT's predictions, thereby removing key bases for these assumptions. What follows is not a small tweak to the philosophical landscape, but a major theoretical reorientation.

2. *The Fate of OPT in Primary Visual Cortex*

2.1 No Broadband Basis Mechanisms

LGN cells tend to be broadly tuned, with selectivities clustering around a small set of directions, yielding axis-like response functions. These clusters are anatomically segregated, with L–M, S–(L+M), and L+M units concentrated in parvo, konio, and magnocellular layers, respectively. These form parallel, independent processing streams for each cardinal axis. Third-stage OPT predicts that V1 recapitulates this kind of organisation by recombining cardinal signals to form new spectrally broadband mechanisms, each tuned to half of an RG or YB axis. These are taken to provide basis signals for encoding the full hue circle: intermediate hues arise through pooled activity across the R/G and Y/B fundamentals. This predicts a two-step cortical organisation. First, new channels should be established, yielding broadband neuronal selectivities that cluster into four relatively discrete groups—potentially anatomically segregated, but at a minimum forming independent processing pathways. Second, more diverse selectivities, if present, should be traceable to pooled activity across these mechanisms, thus only taking forms predictable from the underlying basis functions.

These predictions are not borne out. First, there is scant evidence that new broadband, axis-based mechanisms are established in V1. Input layers preserve the cardinal organisation inherited from LGN, while other layers exhibit continuous chromatic preferences with no clustering around new axes.[27] These preferences reflect complex, often nonlinear

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[27] See Lennie et al. (1990), Wachtler et al. (2003), Johnson et al. (2004), Solomon & Lennie (2005), Conway & Livingstone (2006), Horwitz et al. (2007), Tailby et al. (2008), and Li et al. (2022).

recombinations of cardinal signals, rather than pooled activity across new R/G and Y/B fundamentals. The diversity of response profiles—ranging from broadband to narrowband, and simple nonlinearities to quadratic forms—exceeds what could be generated by combining a small set of broad basis functions. V1 therefore does not repeat the axis-based scheme of LGN, but replaces it with a population code in which selectivities are continuous, heterogeneous, and nonlinear.

In more detail, V1 selectivities fall into fairly discrete groups at input-stages, though these reflect the cardinal channels inherited from LGN, rather than new third-stage mechanisms. Chatterjee and Callaway (2003) used anatomical tracing methods to map LGN afferents—the endpoints of axons projecting from LGN neurons—into V1. They found that afferents from different classes of LGN cell remained anatomically segregated in V1. Magnocellular neurons terminated in layer 4Cα, parvocellular neurons in 4Cβ, and koniocellular neurons projected more sparsely into layers 2, 3, and 4A/B.[28] These afferents were characterised, respectively, as showing no cone-opponency; L/M-cone opponency, with little or no S-cone input; and excitatory or inhibitory S-cone opponency. V1 inputs thus maintain the separation of LGN streams, with the recombinations posited by third-stage models not yet in evidence. If these mechanisms exist, they must involve intracortical circuits that draw on these inputs.

Tailby and colleagues (2008) used single-cell recordings to measure responses to chromatic contrast throughout macaque V1, including input layers (4Cβ and 4A), supragranular (2-3), and infragranular (5-6) layers.[29] Across the whole population, neurons with moderate to strong chromatic selectivity exhibited a continuous spread of preferred hues. Neurons aligned with the L–M axis were proportionally more common in layers 4Cβ and 6, while those aligned with the S–(L+M) axis were more frequent in 4A—patterns consistent with the LGN afferents mapped by Chatterjee and Callaway. These neurons also adapted selectively to modulations along the L–M and S–(L+M) axes, matching the psychophysical signatures of the cardinal mechanisms identified by Krauskopf and colleagues (1982). On this basis, Tailby and colleagues inferred that the fundamental cardinal mechanisms are likely established in the input layers of V1, at or near the LGN terminations.

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[28] Vanni et al. (2020) provide a review.

[29] Their analysis combined data from Solomon et al. (2004), Solomon & Lennie (2005), and Webb et al. (2005).

Beyond the input layers, however, this cardinal axis-based organisation gives way to a more diverse scheme. Tailby and colleagues found that the preferences of neurons in supragranular and infragranular layers spanned the entire DKL hue dimension, including cardinal (0°, 180°, 90°, 270°) and noncardinal (e.g., 45°, 135°) directions. Wachtler and colleagues (2003) reported similar results from single-cell recordings in macaque V1.[30] Preferences ranged continuously but nonuniformly, with the largest peak at 315° or reddish-yellow, and a smaller peak at 45° or purple (Figure X). Many cells preferred directions in the greenish region (~200-250°), while few preferred hues in the S-wavelength region. While the distribution is nonuniform, however, there is no significant clustering around cardinal directions, or unique red (10°), blue (125°), green (220°), or yellow (290°); indeed, these were mostly underrepresented compared to other directions in the same quadrants. This suggests that at post-input stages, V1 encodes chromatic information via populations of neurons with diverse but overlapping tuning curves, completely tiling colour space rather than privileging a small set of directions. This picture is confirmed by work from multiple other groups using different methods, and is also reflected in V2-V4.[31]

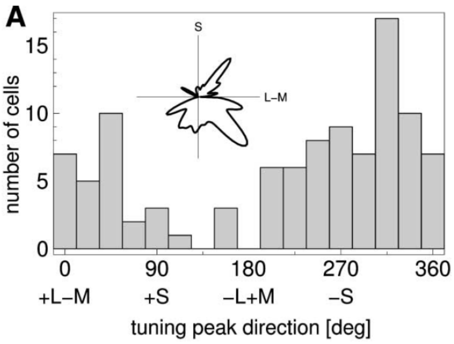

Figure X. Distribution of hue tuning peaks of V1 neurons. [Wachtler et al. (2003)]

De Valois and colleagues (2000) also reported continuous chromatic preferences among 314 cells recorded in V1, though with a slight bias towards the unique hues. Around 72% of LGN cells were tuned within ±15° of the cardinal axes—well above the 33% expected at chance—whereas only 12% fell within ±15° of the unique hues. In V1, by contrast, 66% fell into the unique hue bands, but this was only marginally higher than the 57% chance level.[32] This ‘slight tendency’ (2000: 4999) toward the unique hues is therefore

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[30] Wachtler et al. (2003) aggregated recordings made at various depths in V1, thus reflecting the distribution of chromatic preferences across multiple layers, including input layers.

[31] On V1, see Lennie et al. (1990), Johnson et al. (2004), and Horwitz et al. (2007); on V2-V4, see Gegenfurtner et al. (1997), Kiper et al. (1997), and Zeki (1980).

[32] Because there are four unique hues, the ±15° windows cover 4 × 30° = 120°. Since the V1 cells recorded spanned an effective range of 210°, the expected proportion at chance is 120/210 = 0.57. By contrast, the

far weaker than the axis alignment found in LGN, providing no real support for new axis-based mechanisms. The data rather indicate a diverse population code with a small bias toward hues in certain bands.[33] If these hues enjoy a special perceptual status, it stems from a statistical bias in population activity, not from their forming fundamental basis signals in an opponent code.

Li and colleagues (2022) reinforced this conclusion using high-resolution imaging techniques on macaque V1, targeting supragranular layers 2-3. Cells were stimulated by full-field, temporally modulated, cone-isolating stimuli—thus effectively zero SF. This regime likely isolated activity in single-opponent (SO) cells—on which more later—which prefer low SFs over fine contrasts. They identified distinct cone-opponent functional domains (COFDs), which are regions dominated by one type of cone-opponent input: L–M, M–L, S–(L+M), or (L+M)–S. These are plausibly intracortical projections of cardinal signals established in input layers—the L–M and S–(L+M) mechanisms that Tailby and colleagues (2008) linked to layers 4Cβ and 4A. COFDs are the first known sites in supragranular V1 where inputs from these mechanisms are mapped in distinct zones. This layout facilitates interactions between cone-opponent signals, allowing neurons to combine them within their receptive fields. The intersections of COFDs provide plausible sites for such integration, hence for the formation of new chromatic mechanisms.

As Li and Colleagues (2022: 2) note, third-stage OPT predicts just this kind of ‘mixing’ of cone-opponent signals.[34] But mixing per se is predicted on any theory of cortical colour processing. OPT distinctively expects four fundamental mixtures that reorient cardinal inputs toward the perceptual primaries, establishing OAMs. More diverse selectivities, if present, should arise from pooling over these OAMs. Instead, cells at COFD intersections exhibit a continuous spread of chromatic preferences, indicating that cone-opponent signals are recombined freely, not constrained to four canonical directions. In some areas, cells formed ‘pinwheel’ structures: topographic arrangements in which neighbouring cells tend to prefer neighbouring hues, forming continuous hue maps across the cortical surface.[35] The

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cardinal axes are bipolar, so opposite directions are redundant. This reduces the effective range to 180°, with only 2 × 30° = 60° covered, yielding a chance level of 60/180 = 0.33.

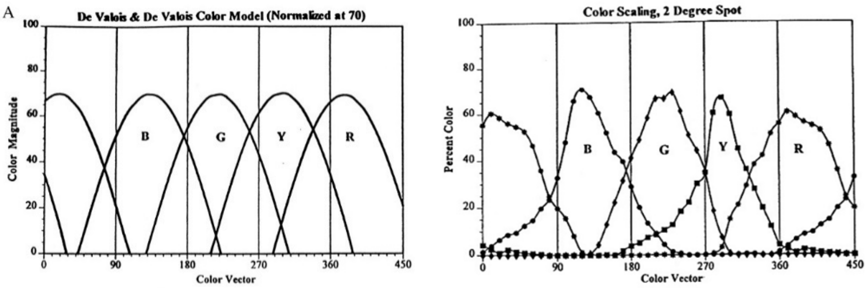
[33] Goddard et al. (2010) report a bias toward lime-magenta in human V1, while Lafer-Sousa et al. (2012) found an orthogonal bias to orange-cyan in macaque V1. While neither bias aligns with unique hues, both correlate well with certain natural scene statistics. Cf. Mollon & Jordan (1997) and Broackes (2011: 619-626).

[34] Cottaris & De Valois (1998: 896) also emphasise mixing as a distinguishing mark of third-stage mechanisms.

[35] Xiao et al. (2007) and Chatterjee et al. (2021) also found hue maps in supragranular V1 using intrinsic optical signal imaging and two-photon calcium imaging, respectively. These studies both used uniform field stimuli, supporting the claim that V1 hue maps comprise SO populations. Cf. Parkes et al. (2009) and Garg et al. (2019).

maps were centred on points where orthogonal COFDs converged, suggesting they emerge directly from the recombination of cardinal inputs. There is no evidence that these structures privilege the unique hues or that new axes are established. Supragranular V1 therefore does not implement an axis-coordinate format: it establishes a qualitatively different representational scheme, exploiting spatial layouts of hue preferences across cortex, providing complete coverage of the spectrum. This topographic format is not restricted to V1, moreover, but is elaborated in V2, V4, and beyond.[36]

OAMs are supposed to have spectrally broad response functions—roughly sinusoidal curves with symmetrical lobes spanning about half of colour space. De Valois and De Valois's (1993) model 'red' mechanism, for instance, peaks near unique red but responds substantially through orange and purple, significantly overlapping both yellow and blue regions. Such tuning is the hallmark of a linear, axis-based mechanism: when a neuron sums signals along a fixed direction in cone-contrast space (e.g., L–M), it responds to any hue with a component along that direction, yielding a wide and smooth response curve. This is what we find in LGN, where most neurons show broad, approximately linear combinations of cone inputs; yet in V1, such profiles are rare. Using isoresponse methods, Horwitz and Hass (2012) found that only about half of neurons in macaque V1 were even approximately linear, and many of these were dominated by luminance contrast. The chromatically selective cells divided into two groups: one tuned near the L–M axis, another dispersed across colour space without clear clustering.[37] In short, the broad, linear responses that would support new axis-based mechanisms in V1 are both scarce and misaligned.



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[36] On hue maps in V2, see Xiao et al. (2003) and Lim et al. (2009); for V4, see Tanigawa et al. (2010), Li et al. (2014), and Liu et al. (2020). These studies use low- to medium-frequency isoluminant gratings rather than full-field stimuli, which could still be expected to favour low-SF SO populations. For related work, see Lu & Roe (2008), Brouwer & Heeger (2009), Conway (2014), Zaidi & Conway (2019), and Du et al. (2022).

[37] Hanazawa et al. (2000) similarly reported that the simplest linear V1 neurons tended to cluster around the cardinal axes—particularly 0°, 90°, and 180°—though had broader curves than LGN. Hansen & Gegenfurtner (2006) found evidence for 16 chromatic detection mechanisms with linear response functions, equally distributed around the isoluminant hue circle. See also Gegenfurtner & Ennis (2015: 77-79).

Figure X. (a) Chromatic response curves predicted by third-stage model, (b) hue-scaling results [De Valois et al. (2000)]

Moreover, chromatic cells in V1 typically show nonlinear tuning. A first kind of nonlinearity—*compressive* or *expansive*—changes the shape of an otherwise sinusoidal function. Wachtler and colleagues (2003) reported that most chromatic cells exhibited such profiles, with either broadened (compressive) or narrowed (expansive) sinusoidal tuning curves. Compressive cells are too broad to encode opponent axes: a 'red' mechanism with a broadened response curve would bleed too far into yellow and blue. Expansive cells are generally too narrow, giving insufficient coverage outside the zone of their optimal hues. Only a small minority of cells occupy the 'Goldilocks' zone of intermediate breadth, and even these are scattered throughout colour space rather than concentrated near the perceptual primaries.[38] Moreover, the trend toward narrower tuning continues in areas V2 and V4/IT, making them still less likely candidates for axis-encoding OAMs.[39]

Compressive and expansive nonlinearities already deform what should be axis-like, sinusoidal tuning curves by flattening or sharpening their peaks. Many V1 neurons depart even further from this geometry. Horwitz and Hass (2012) found that many were best fit by quadratic functions, forming ellipsoidal or cup-shaped isoresponse surfaces that isolate small regions of cone-contrast space. In effect, the broad sinusoid of an axis-based channel collapses into a local basin. These neurons no longer respond along extended directions through cone-contrast space, giving graded responses across a wide range of hues: they pick out small islands of selectivity, responding strongly only within a narrow hue neighbourhood.[40] The result is far from an opponent axis code—closer to a mosaic of locally tuned chromatic mechanisms.

An advocate of OPT might argue that an opponent axis structure is imposed by decoder mechanisms that 'read off' R/G and Y/B values from patterns of activity across these diverse, nonlinear populations. This view is underspecified without a concrete decoding model—currently lacking—but the basic idea is clear enough: LGN afferent signals are first passed through populations with diverse, narrowband selectivities, whereafter a decoder

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[38] De Valois & De Valois (2000) present evidence that many chromatic cells fall into this range, prompting a revised third-stage model with more narrowly-tuned OAMs. This was also prompted by new hue-scaling data (De Valois et al., 1997, 2000), which suggested narrower response curves than earlier reported. See also Cottaris & De Valois (1998).

[39] On V2, see Levitt et al. (1994) and Kiper et al. (1997); on V4/IT, see Conway (2014), Zaidi & Conway (2019), and Zeki (1980).

[40] The 'type 3' chromatic cells of Hanazawa et al. (2000) similarly surrounded and 'locked in' small regions in CIE chromaticity space, including intermediate hues such as orange and purple

compresses these patterns of activity in a low-dimensional readout structured by RG/YB axes. This gambit offers no succour to OPT. First, it still predicts fixed, broadband basis mechanisms aligned with R, G, Y, and B; the difference is that these are now modelled as stable decoders of diverse population activity, rather than immediate transformers of cardinal signals. Yet there is no evidence of such mechanisms in V1. Of course, the decoders might live downstream in V2 or V4, but these areas exhibit the same signatures as V1, with continuous hue maps and increasingly narrowband tuning. While speculative, this suggests that V1 populations feed mechanisms with the same topographic organisation—performing map-to-map transformations, rather than map-to-channel as OPT requires.[41]

Second, even if an RG/YB readout is extracted from the V1 (likewise, V2/V4) population, there is no inevitability to its opponent structure. The effective geometry of such readouts depends on how the decoder samples and weights the manifold of responses across the population. Extant models treat these as flexible and task-dependent decoding strategies, rather than fixed bases.[42] Some decoding strategies may yield an opponent RG/YB geometry, but many will not.[43] Absenting the strong architectural constraints of distinct channels, there is no physiological basis for privileging one geometry over another. Yet OPT requires that the RG/YB axes are favoured by design, not merely an incidental low-dimensional fit. Unless evidence for such favour emerges, the population gambit offers OPT no respite.

2.2 No Achromatic Segregation

A core commitment of OPT is that chromatic and achromatic signals are carried by separate channels. Third-stage models predict that early cortex should begin to decouple these signals, establishing a dedicated luminance pathway. De Valois and De Valois (1993) propose a specific route: cortical neurons should pool cone-opponent signals—L–M, M–L, and S–(L+M)—so that their chromatic components cancel, leaving a purely achromatic output. If sound, V1 would mark the stage at which chromatic and achromatic signals finally disentangle.

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[41] For evidence pointing in this direction, see Brouwer & Heeger (2009) and Du et al. (2022).

[42] Jazayeri & Movshon (2006) is a classic example. For an alternative philosophical take, see Shea (2018: 94ff).

[43] Bosten & Boehm (2014) found that subjects can adopt arbitrary fundamentals—hence, effective axis structures—in hue scaling tasks, rating proportions of teal, purple, orange, and lime just as well as RG/YB. For further evidence of contextual variation in the effective geometry of colour representation, see Webster & Mollon (1994), Ekroll et al. (2002), Hansen et al. (2007), Webster & Leonard (2008), Niederée, R. (2010), C. Tajima et al. (2016), S. Tajima et al. (2017), and discussion below.

Empirical evidence points the other way. Parvo and koniocellular inputs to V1 already multiplex chromatic and luminance information, and V1 neurons preserve—indeed, often extend and exploit—that mixture rather than dissolving it. Johnson and colleagues (2004) found that of 139 luminance-preferring neurons, only 12% were cone-opponent, and most had negligible S-cone weight, hence little or no contribution from the proposed S–(L+M) term. The L- and M-cone weights were broadly distributed, rarely forming the balanced ratios required to cancel chromatic components. Moreover, as Lee (2019: 160) observes, V1 responses are half-wave rectified: their negative outputs are clipped, making cancellation impossible. Summing L–M and M–L therefore yields overall chromatic energy, not a neutral luminance signal. The proposed route for decoupling luminance thus fails in principle, as well as lacking evidence in practice.

Far from establishing a separate luminance channel from cone-opponent inputs, V1 compounds the mixed selectivity inherited from LGN.[44] Lennie and colleagues (1990) found that few V1 cells responded solely to chromatic modulation, and these were mainly concentrated in input layers. Elsewhere, the majority of chromatic cells showed substantial luminance selectivity.[45] Johnson and colleagues (2004) likewise reported that neurons with the strongest chromatic selectivity clustered around equal and opposite L- and M-cone weights, resembling parvocellular LGN, thus possibly relaying LGN inputs. In contrast, the majority of neurons in layers 2-3 combined chromatic and luminance drives in varying proportions.[46]

Complementary findings by Li and colleagues (2015) refine this picture. Using drifting gratings that isolated luminance, chromatic, or combined contrast, they found that cells in superficial V1 tended to prefer either luminance or chromatic contrast, whereas deeper layers preferred the combination. Responses were well predicted by a weighted sum of each neuron’s luminance-only and chromatic-only tuning, often with additional

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[44] Akins & Hahn (2014: 128-129, 134, 157) discuss some details of combined chromatic-luminance coding.

[45] Lennie et al. (1990) questioned whether chromatic-luminance cells contribute to colour perception, based on the apriori assumption that cells responding most to equiluminant chromatic contrast would play the major role. Conway (2001: 2781-2782) makes a similar argument. For discussion of how to define a ‘chromatic’ cell, see Schluppeck & Engel (2002), Gegenfurtner (2003: 565-566), Johnson et al. (2004: 2511-2512), and Gegenfurtner & Ennis (2015: 80-84).

[46] Numerous studies report similar findings in V1 (Gouras & Kruger, 1979; Thorell et al., 1984; Conway, 2001; Shapley & Hawken, 2002; Wachtler et al., 2003; Hass & Horwitz, 2013; Li et al., 2015; Garg et al., 2019), as well as V2 (Kiper et al., 2001), V4 (Bushnell et al., 2011) and IT (Harada et al., 2009; Namima et al., 2014).

nonlinearities. Overall, V1 exhibits a graded continuum from pure- to mixed-selectivity, with deeper layers showing stronger integration of magno and parvo/koniocellular inputs.[47]

Psychophysics reveals a parallel pattern. At detection threshold, chromatic and achromatic mechanisms behave largely independently: cross-masking with achromatic noise scarcely affects chromatic detection, and vice versa, implying separate mechanisms.[48] Yet above threshold, strong interactions emerge. Suprathreshold luminance contrast can facilitate chromatic detection, and brightness contrast at borders can inhibit chromatic induction.[49] Adapting to a bright red/dim green grating causes aftereffects specific to this chromatic-luminance axis: luminance increments appear greenish and decrements reddish, while equiluminant reds and greens appear respectively darker and lighter.[50] Classic appearance phenomena, such as Bezold-Brucke (Purdy, 1931) and Helmholtz-Kohlrausch (Corney et al., 2009) effects, show that perceived hue varies systematically with luminance. Overall, the threshold data support segregation, but as contrast increases, so does colour-luminance interaction, undermining the idea of functionally independent chromatic and achromatic mechanisms.

In sum, the pattern from physiology to perception is strikingly consistent. Where OPT predicts early segregation of chromatic and achromatic signals, the evidence shows pervasive mixture. Functional independence holds only at the lowest contrasts and dissolves as stimulus strength increases. This mixed selectivity nonetheless admits two interpretations, with different consequences for OPT. One possibility is that it reflects imperfect circuitry rather than genuine integration. Take a nominal double-opponent (DO) cell with a +L, –M, –S centre and –L, +M, +S surround. As Conway (2001) notes, when centre and surround are perfectly balanced, modulation along the L+M axis yields no response: +L in the centre is nulled by –L in the surround, and –M by +M. Conversely, any imbalance will leave a residual L+M term, so the cell will respond to black-white gratings as well as red-green. On this reading, mixed selectivity is not an architectural feature, but a by-product of receptive field

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[47] Mullen et al. (2015) found strong evidence of integrated chromatic-achromatic activity throughout visual cortex using fMRI adaptation, though this was strongest in V1 and V2, and decreased in V4 and VO. Xing et al. (2015) also report brightness-colour interactions in V1.

[48] See Gegenfurtner & Kiper (1992), Mullen & Losada (1994), Losada & Mullen (1995), Sankeralli & Mullen (1997), and Giulianini & Eskew (1998).

[49] On detection, see De Valois & Switkes (1983), Switkes et al (1988), Eskew et al. (1991), Horwitz et al. (2005), Mullen et al. (2014), and Kim & Mullen (2016). On induction, see Gordon & Shapley (2006).

[50] See Webster & Mollon (1994) and Webster & Malkoc (2000).

imbalances—awkward for OPT, but consistent with an ideal of mechanisms that aim at segregation and only 'leak' luminance when weights are mismatched.[51]

Alternatively, mixed selectivity might be a functional feature of cortical architecture—both for SO and DO populations. Recent physiology supports this second view. For SO-leaning, uniform-field conditions, Li and colleagues (2022) found that ON- and OFF-luminance domains overlap significantly with cone-opponent COFDs in superficial V1. The luminance domains (magnocellular driven) and COFDs (parvo/koniocellular driven) are laid out in an interdigitated pattern—precisely the arrangement expected if chromatic and luminance signals interact within single receptive fields. Consider an SO 'ON-red' unit (+L centre, −M surround) that is half-wave rectified—its negative portion clipped, so it fires for red and stays silent for green. Under equiluminant red-green modulation, adding an ON- or OFF-luminance input does nothing, as there is no luminance change to drive it. Under uniform mixed modulation, however, these inputs produce opposite effects. With bright red-dim green modulation, ON-luminance boosts the red phase, keeping the green phase silent, effectively sharpening chromatic selectivity; OFF-luminance attenuates the red phase and yields a residual green response, thus weakening chromatic selectivity. Conversely, with dim red-bright green modulation, OFF-luminance boosts red and keeps green silent, while ON-luminance attenuates red and drives a residual green response. Intuitively, because the unit 'sees' nothing chromatically in the green phase, the luminance input alone decides whether the green half 'looks' like red or not. ON-luminance input sharpens the red response when the green half is bright and flattens it when green is dim; OFF-luminance does the opposite.

Pairing ON- and OFF-luminance coupled ON-red subpopulations facilitates an illumination-invariant chromatic readout. Consider a uniform red patch under rapidly varying illumination, alternating luminance increments and decrements as on a cloudy day. In increment phases, ON-luminance coupled units respond strongly; decrement phases stimulate OFF-luminance coupled units. Summing or pooling across these pairs effectively cancels the luminance terms, yielding chromatic signals that are both gain-boosted—increased response slopes for weakly preferred stimuli—and near-constant despite the noise. Luminance

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[51] Johnson & Mullen (2016: 204) suggest that such imbalances might be inherited from the variable spatiotemporal characteristics of LGN receptive fields. Cf. Horwitz et al. (2007) and Hass and Horwitz (2013).

coupling is thus functionally advantageous, sharpening and stabilising chromatic responses to uniform fields under achromatic variations in illumination.[52]

Similar points apply to DO units (e.g., +L–M centre, –L+M surround), which are selective for coloured patterns and edges—on which more presently. When chromatic and luminance edges co-occur, as is frequent in natural scenes,[53] coupling ON-luminance to such a unit strengthens responses to bright red/dim green edges relative to equiluminant red/green. OFF-luminance does the same for dim red/bright green. A menu of ON/OFF-coupled DO units therefore ensures baseline selectivity for pure chromatic and luminance edges, while sharpening chromatic selectivity for mixed-polarity edges. Here, luminance is not merely multiplexed with chromatic signals, in the way shape and colour content is carried by different aspects of a single colour chit.[54] Instead, these units encode *chromatic × luminance* contents—intuitively, *bright red versus dim green*, rather than *red versus green* plus *bright versus dim*. This has important functional consequences: rather than one vehicle carrying separable chromatic and luminance values, the luminance input changes the shape of the chromatic tuning function. Additivity therefore fails, as the response function includes cross-terms for the chromatic-luminance interaction, rather than simply adding chromatic and luminance terms. This is like a colour chit with fluorescent paint that turns vivid red only under strong illumination: it does not encode *red* simpliciter, rather *vivid red under strong illumination*.

Overall, these points suggest that mixed selectivity is not a design flaw but a flexible resource, increasing coding robustness across the empirically observed range of illumination conditions and chromatic and luminance edges. This significantly undermines Achromatic Segregation: instead of forming a dedicated luminance channel from cone-opponent signals, early cortex entrenches chromatic-luminance interactions in both SO and DO populations, producing codes well adapted to the variability in natural scenes.

2.3 No Spatial-Objectual Invariance

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[52] Johnson et al. (2004: 2510) and Nunez et al. (2022: 4381) offer a different though compatible perspective, on which SO cells signal the spectral characteristics of illumination. Bannert & Bartels (2017) found evidence for illumination-invariant chromatic signals in V1 and V4a using multivariate fMRI pattern analysis.

[53] See Zhou & Mel (2008) and Fine et al. (2003). Hansen & Gegenfurtner (2009) found that, while chromatic and luminance edges typically cooccurred, chromatic contrast was not predicted by luminance contrast, making chromatic edge information nonredundant. See also Akins & Hahn (2014: 140ff).

[54] The standard engineering example of multiplexing is to use the wavelength and amplitude of a signal—which bear no direct relationship—to encode different properties.

In its canonical form, OPT conceives chromatic coding as pointwise and form-blind. At each point in the retinal image, OAMs transform cone signals to three opponent values (RG, YB, WBl), in ways that are insensitive to the spatial layout or structure of the stimulus. On this view, chromatic encoding is invariant under changes in spatial-objectual form: OAMs specify coordinates in the same opponent coordinate frame across all contexts. Contextual effects such as adaptation, contrast, and assimilation can then be explained by gain changes within each mechanism, scaling outputs without altering the underlying frame.[55] Whatever the stimulus, every location in the image is described by values in a fixed opponent space.

Empirical evidence indicates otherwise. Chromatic signals in V1 are not form-invariant but systematically indexed by parameters such as orientation and SF. Using single-unit recordings in macaque V1, Leventhal and colleagues (1995) found that nearly all neurons in supragranular layers were orientation-selective, including those strongly modulated by chromatic contrast. These selectivities spanned the full range of orientations and SFs, though chromatic cells tended to prefer lower SFs than luminance cells. Johnson and colleagues (2001, 2008) refined this picture, showing that around half of supragranular neurons responded to both chromatic and luminance contrast, and these were almost always orientation selective.

This pattern reflects their DO structure, which combines chromatic and spatial opponency. A DO unit with a +L–M centre and –L+M surround, for instance, responds strongly to spatial contrasts in L–M and weakly to uniform fields. Many such RFs are elongated rather than circular, producing orientation selectivity and bandpass tuning: because excitation and inhibition alternate along the RF's long axis, the unit responds maximally to gratings with frequencies matching that alternation, and less to finer or coarser patterns. This is precisely the behaviour observed in chromatic-luminance cells. By contrast, a small minority of neurons preferred only chromatic contrast and showed little orientation selectivity. These are likely SO cells, which yield chromatic but not spatial opponency, thus responding best to uniform fields rather than fine contrasts.

A deflationary reading treats these orientation-selective, bandpass DO cells as serving form rather than colour perception—edge detectors that happen to use cone-opponent

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[55] For discussion of gain control, see Webster & Mollon (1994: 2017-2019), Delahunt & Brainard (2000), Solomon & Lennie (2005), and Stockman & Brainard (2010: 10-11, 15-26).

signals.[56] Yet their behaviour undermines that view. Many are *phase-selective*, responding strongly to chromatic contrasts with a specific polarity, such as red-left/green-right, but not the reverse. Such selectivity encodes the chromatic composition of the edge, not a generic 'edge present' signal.[57] Chromatic edge signals feature in explanations of perceptual phenomena such as filling-in, the watercolour illusion, and colour constancy.[58] These mechanisms therefore contribute centrally to colour perception, not merely form perception.

Psychophysical results likewise implicate DO mechanisms in colour appearance itself. In a perceptual scaling study, Nunez and colleagues (2018) found that checkerboard patterns were judged more saturated than uniform fields with equal space-average cone contrast—an effect expected if DO cells, tuned to spatial chromatic contrast, contribute directly to perceived saturation. SO cells, in contrast, should respond similarly to both stimuli, making them unsuitable to explain the results.[59] Werner (2003) similarly showed that chromatic adaptation depends on the form of a luminance-defined pattern in the surround: adaptation was orientation-selective, strongest when target and surround matched orientation; and bandpass, peaking when the width of the target matched the surround frequency.[60] Given that the surround pattern was luminance-defined, these are chromatic-luminance interactions. DO cells have exactly the right features—orientation-selective, bandpass, mixed chromatic-luminance tuning—to explain these effects, strongly implicating them in colour perception.[61]

A conservative extension of OPT could try to accommodate these findings through form-dependent gain control. The idea is that surround orientation or SF might influence how strongly each opponent mechanism responds, without altering the opponent coordinate frame

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[56] A *locus classicus* for the deflationary line is Livingstone & Hubel (1984), who reported DO cells with circular-symmetric RFs, thus little orientation-selectivity, in cytochrome oxidase blobs of V1—often considered important for colour processing. They also found cells with joint chromatic-orientation selectivity in interblobs, which they surmised were purely form-related.

[57] See Zhou et al. (2000), Friedman et al. (2003), Rudd & Zemach (2007), Seymour et al. (2016), and Davies (2021, 2022). Unlike these so-called 'simple' DO cells, 'complex' cells pool multiple directions of chromatic or achromatic contrast, increasing signal-to-noise ratios for edges while losing information about their chromatic content; see Lennie et al. (1990), Johnson et al. (2004), Conway & Livingstone (2006), Horwitz et al. (2007).

[58] On filling-in, see Sasaki & Watanabe (2004), Komatsu (2006), Huang & Paradiso (2008), Zweig et al. (2015), Hong & Tong (2017), and Gerardin et al. (2018). On the watercolour illusion, see Pinna et al. (2001) and Pinna & Grossberg (2005). On constancy, see Hurlbert & Wolf (2004), Kentridge et al. (2004), and Davies (2022).

[59] On V1 responses to colour saturation, compare Hanazawa et al. (2000) and Li et al. (2022).

[60] Zaidi et al. (1998) reports similar results. Barnes et al. (1999) and Wolf & Hurlbert (2002) also found that chromatic induction depends on relations between frequency and texture in test and surround. Another prominent case is the tilt aftereffect and tilt illusion, discussed by Flanagan et al. (1990) and Clifford et al. (2003). For other interactions, see Monnier & Shevell (2003), Shevell & Monnier (2005).

[61] Werner et al. (2000) reported marked differences in adaptation to structured patterns versus uniform fields: the former operates at faster timescales, shows heightened selectivity for medium wavelengths, and varies with pattern complexity. This suggests that different mechanisms subserve each kind of adaptation.

itself. For instance, an R mechanism might be up-weighted when surround contrast runs vertically and down-weighted when it runs horizontally, introducing sensitivity to the surround's orientation. Stimuli are still encoded by values along a fixed RG axis; only the signal magnitudes shift with local orientation. On this view, form acts as a source of weighting, not as a new encoding dimension: the geometry of the chromatic code remains fixed while its amplitudes vary with context.

This move fails for a simple reason: orientation- and frequency-selective adaptation requires that chromatic signals themselves be indexed by orientation and frequency. Form-dependent gain control can scale values on a fixed RG axis, but it cannot produce form-selectivity unless the underlying code distinguishes contrasts at different orientations and frequencies. To see why, suppose that RG values at a location x are unindexed by form, but scaled by a factor determined by a surround with orientation θ. Consider two equiluminant red bars at x, with orientations θ and θ+90°. Suppose that the surround up-weights the R signal at x. Because the surround is fixed, this scaling factor is constant; if the R signal is not form-indexed, the values will be identical for the two bars—contrary to the finding that adaptation is orientation-selective. The surround should exert a greater influence on R when the bar is at θ than θ+90°, but that requires R to be indexed by orientation. The same applies, mutatis mutandis, for SF.

The data therefore force a change not merely in gain but in the chromatic code: at a minimum, there must be multiple form-indexed subchannels—$R_{\theta,f}$, $G_{\theta,f}$, $Y_{\theta,f}$, $B_{\theta,f}$—each tuned to a specific orientation θ and frequency f bands. Contextual modulation then acts selectively on matching subchannels, enhancing or attenuating chromatic signals that share the surround's structure. A surround with orientation θ will modulate activity in R_θ more than $R_{\theta+90}$, producing orientation-selective adaptation. Functionally, adaptation works like an equaliser that modulates chromatic contrast within each spatial band, rather than a single dimmer applied uniformly to fixed opponent channels.

This already undermines OPT's prediction of Spatial-Objectual Invariance. Yet physiology pushes further. The form-indexed mechanisms found in V1 do not cluster around a canonical pair of axes: as already shown, they span a wide range of hue and chromatic-luminance preferences. The data therefore do not favour form-indexed R/G and Y/B subchannels: they point instead to a bank of mechanisms tuned to diverse combinations of hue, luminance, orientation, and frequency. This bank functions as a set of filters, each capturing a different component of the spatial-objectual-chromatic structure at each location. Collectively, these filters generate a high-dimensional coding space, in which continuously varying hue and chromatic-luminance selectivities are interleaved with spatial selectivities. As above, these filters are not mere multiplexers: they encode *chromatic* × *luminance* × *form* contents—structured combinations like *bright orange-dark cyan contrast at vertical orientation and high frequency*, not merely *orange-cyan contrast*, and certainly not just *red-green* or *yellow-blue*. In sum, the early cortical chromatic code is not just form-indexed but diverse and many-dimensional—far from OPT's fixed three-axis ideal.

An advocate of OPT might argue that a form-invariant 3D structure is imposed downstream by decoders that 'read off' opponent values from activity across the form-indexed bank. Yet for any high-dimensional encoder, linear low-dimensional readouts are ensemble-relative. Think of the encoder as an *n*-dimensional grid of filters, encoding hue × luminance × orientation × SF ×… Each stimulus ensemble activates a characteristic subset of this grid and sets its gains via adaptation or normalisation. A linear decoder fits a 3D readout by analysing the response covariance of the currently recruited population.[62] This covariance changes when the ensemble changes, because ensembles with different colours, illumination, orientations, and SFs will recruit different parts of grid and set their gains in different ways. As the covariance changes, so will the readout's structure: the axes (principle directions), metric (rule for distances and angles), and therefore orthogonality (right angle relations defined by metric) and scaling (units or gains along each axis) all warp with context. Some ensembles may yield structures that align with RG/YB, but in general they will not. The population gambit therefore does not save OPT's fixed opponent geometry: it supplants it with context-dependent projections.

The encoder/decoder framework invites an even deeper departure from OPT's 3D template. Once we lose the strong architectural constraints of three cone-opponent channels, there is no reason a decoder must return exactly three dimensions, or the same three across contexts. The encoder supplies *n*-dimensional chromatic × luminance × form signals; decoders can be flexible and task-dependent, sampling and weighting this manifold differently for different purposes. In some regimes—such as uniform fields, neutral illumination—a 3D projection may be a good summary; though even then, not inevitably

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[62] On covariance methods for dimension reduction in a population coding framework, see Cunningham & Yu (2014), Stringer et al. (2019), and Williamson et al. (2019). On context-dependent computations in a population setting, see Mante et al. (2013), Remington et al. (2018), and Semedo et al. (2019). On the significance of mixed selectivity in relation to task-dependent decoding, see Rigotti et al. (2013), Kobak et al. (2016).

structured by RG/YB/WBl axes. In many natural contexts, however, higher-dimensional readouts are both available and useful. For example, a decoder might extract explicitly form-indexed structure like *bright orange at vertical orientation, mid-frequency, with dark cyan surround*; illumination-indexed structure like *dark green under bright bluish illumination*; and perhaps transparency-indexed structure like *dark yellow behind bright reddish filter*. Psychophysical scaling with complex surrounds, variable illumination, and transparency indeed points to representations with four or more dimensions in such contexts.[63] Notwithstanding the inconvertible evidence for retinal trichromacy and LGN's three cone-opponent channels, these data support a cortical code with greater flexibility and often higher dimensionality.

The upshot is that 'colour representation' has no single, three-dimensional interpretation: it picks out a family of context-dependent projections from a high-dimensional manifold of chromatic × luminance × form signals, onto lower-dimensional spaces for representing coloured objects under varying illumination. In the limiting case of no spatial-objectual structure and uniform, neutral illumination, a three-coordinate summary may be serviceable. In the general case, though, the geometry rotates and warps, and the dimensionality expands whenever the scene's principal variations demand it. Opponent-colour representations, when they appear, are merely convenient readouts, not elemental vehicles.

3. *Reorienting Philosophical Views on Colour Representation*

The previous section demonstrates that OPT is inadequate to describe early cortical chromatic processing. Research in V1 does not indicate a small set of broadband OAMs marked by achromatic segregation and form-invariance. Instead, it reveals a dizzying array of mechanisms, characterised by diverse and specific hue preferences, often nonlinear profiles, variable chromatic-luminance selectivity, and form-indexed responses—right where OPT's third-stage transformations should begin.

This forces a reappraisal of common philosophical assumptions about colour representation. Just as painters produce the full gamut of colours by mixing a few primaries,

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[63] For colour scaling under variable surrounds, see Evans (1974), Ekroll et al. (2002), MacLeod (2003), and Niederée (2010); for variable illumination, see Katz (1911/1935), Brainard et al. (1997), Logvinenko & Maloney (2006), and Tokunaga & Logvinenko (2010a,b), and Hilbert (2005), Jagnow (2009, 2010), and Davies (2016, 2025) for philosophical discussion. On transparency, see Khang & Zaidi (2002), Faul & Ekroll (2002, 2011), Faul (2017), and Ennis & Doerschner (2021).

so philosophers have sought to ground the full range of colour experience in a few fundamental vehicles. Contemporary OPT invites the view that colour representations have a simple three-part structure, with components that represent values along RG, YB, and WBl axes. This format factorises chromatic and achromatic components, with separate vehicles for hue and brightness/lightness content.[64] These vehicles are also form-blind, being insensitive to spatial-objectual form at the point of encoding—continuing a long tradition of treating colour representation as pre-objectual. From the early modern period to early twentieth century empiricism, colour experience was often rooted in a 'sensory core' that was both metaphysically and epistemologically prior to object perception. While few now endorse this view, it has left an indelible mark on perceptual theory: where colour sensations have been replaced by representations, these standardly remain pure colour vehicles—encoding colour per se rather than coloured forms.

The failure of OPT's empirical predictions undermines these assumptions and suggests new directions. Drawing such implications involves some speculative bridging between physiology and representational-level description. But if philosophers inferred an opponent format from 1980s retinogeniculate physiology, parity of reasoning supports moving from current cortical physiology to an altogether different scheme.[65] More precisely, different *schemes*: the data support a plurality of formats over OPT's vehicular monism.[66] Another potential concern is that this work focuses on early cortex, deferring transformations in V2-V4 and IT—areas more often linked with colour perception. Early cortex therefore may seem a poor site to base inferences about perceptual representational format.[67] Yet the signatures observed in V1—diversity, specificity, mixed selectivity, form-indexing—appear throughout cortex, indicating systemic coding strategies rather than regional quirks. It seems unlikely, moreover, that there is one privileged site—a 'colour centre'—for the perceptual

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[64] The hedge on 'brightness/lightness' is significant, as it is unclear how OPT's achromatic channel is supposed to encode both aspects. Hardin (1988: 114ff) focuses his discussion of colour structure on brightness—which applies to colours perceived in the aperture mode—suggesting that the points can be 'paralleled for *related*, or surface, colours.' He provides no details, however, as to how a channel that encodes bright-dim values could also represent white-black. These issues are beyond the present scope.

[65] Brette (2019) cautions against inferring representational format from neural code, emphasising the context-dependent nature of correlational information in neuronal spiking rates. Yet there are rigorous theories of representation that explicitly account for such context-dependence; for example, see Shea (2018: 97-110).

[66] Quilty-Dunn (2020; 2023) offers a pluralistic view of perceptual representational formats; cf. Burnston & Cohen (2012, 2015).

[67] MacLeod (2010: 153) is sceptical, claiming that 'cells in [V1] exhibit a practically infinite variety in their functional organization, … with no indication that any one cell has an independent role in perception, or of what its role would be if it did.'

representation of colour;[68] rather, complex phenomena like contrast, constancy, adaptation, induction, and transparency are explained piecemeal by representations at multiple stages, including V1. Early cortex thus has much to teach us about the format of perceptual representation.

In reformist spirit, I therefore propose the following theses:

I. *Cardinal Detection Channels*: under low-contrast stimulation, early cortex recruits a channel-based format, whereby chromatic and achromatic contrasts are represented by coordinate values along cardinal axes, L–M, S–(L+M), and L+M.

II. *Topographic Hue Maps*: under low-frequency spatial structure, early cortex implements a topographic format, whereby relations between hues are represented by spatial relations between neurons with continuously varying chromatic preferences. Successive cortical stages decode hue map representations, producing readouts in other, increasingly complete and balanced hue map formats.

III. *Filter Banks*: for structured input (edges, gratings, textures, and so forth), early cortex recruits a bank of filters tuned to hue × luminance × orientation × spatial frequency, whereby stimulus ensembles are represented by patterns of activity across the bank. Decoders of these representations produce context-dependent readouts with varying geometries, with dimensions, axes, and metric shaped by task demands.

Concerning Cardinal Detection Channels, the psychophysical detection data implicate adaptable mechanisms that represent stimuli in a cardinal axis-coordinate format. The physiological data suggest these mechanisms are implemented at early-stage V1, at or near the LGN afferents (Tailby et al., 2008). Evidence for 'higher-order' detection mechanisms tuned to noncardinal directions complicates the picture, suggesting cardinal mechanisms are not the only means by which early cortex detects small contrasts. Nonetheless, higher-order effects are secondary in character compared to cardinal effects, suggesting that cardinal mechanisms play a privileged role in detection.[69] In any event, as far as the current evidence goes, these cardinal detection mechanisms are the first and last instances of a channel-based format for colour representation in visual cortex. This format primarily subserves detection

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[68] Though once popular, Zeki's (1980, 1983) claim that V4 is a colour centre has been largely discredited: see Heywood et al. (1992), Cowey & Heywood (1995), Huxlin et al. (2000), Gegenfurtner (2003: 569-570), Tootell et al. (2004), and Shapley & Hawken (2011: 713-715). Recent research indicates a significant role for IT in colour perception—though few now assume a modular view; see Conway (2018) for a review.

[69] See Eskew (2009), Stockman & Brainard (2010), Gegenfurtner & Ennis (2015) for reviews.

rather than 'appearance'-related phenomena, dashing OPT's hopes for all-purpose colour vehicles.

As for Topographic Hue Maps, for uniform or low-SF stimuli, hues are represented by vehicles that exploit structural correspondences between the spatial layout of selectivities within the vehicle and certain hue relations. In some cases, the vehicles exploit pinwheel arrangements, redolent of cortical formats used to represent other features—notably orientation.[70] In other cases, selectivities are arranged approximately linearly rather than circularly. One striking feature of these vehicles is that all hues are created equal, in the sense that there is no functional difference in how different parts of the vehicle represent. Crucially, there are no 'secondary' parts that represent by pooling activity from other parts, which thus might be termed 'primary.' 'Secondary' hues like orange and purple, and 'primary' hues like red, yellow, and blue, are represented by functionally undifferentiated vehicle-parts. Unlike channels that represent a privileged set of axes, then, these topographic formats do not emphasise any particular direction(s) of selectivity.

To be clear, these topographic formats do encode opponent relations; they just do not privilege any particular pairs of opponent hues. Whenever units tile all directions through the DKL origin, any pair of units tuned to opposite directions will behave as opponents. Think of a unit's preference as a vector in DKL space, built from a linear combination of the cardinal signals (x = L–M, y = S–(L+M), z = L+M), in the form $p = \alpha x + \beta y + \gamma z$. The opposite preference corresponds to the same vector but with reverse sign: $-p = -(\alpha x + \beta y + \gamma z)$. For a pair of half-wave rectified units tuned to those opposite directions, any stimulus that drives one will leave the other silent; they will not co-activate. This holds whether the pair is red versus green, or orange versus cyan, provided they lie on a single line through the origin. The upshot is that opponency is a property of many chromatic pairs, not a privilege of just RG and YB.[71] This is reflected in cortical hue maps, which do not structurally encode any major opponent relations; rather, they roughly maximise the spatial distance between any pairs of hues lying in opposite directions. Opponency lives on—as one would hope and expect—but in a considerably weakened and generalised form.

Finally, concerning Filter Banks, patterned stimuli are represented by activity in populations with a wide range of mixed selectivities. This format encodes different

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[70] See Bonhoeffer & Grinvald (1991), Maldonado et al. (1997), and Ohki et al. (2006).

[71] Compare De Valois & De Valois (1993: 1060), who predict privileged opponency relations between third-stage, half-wave rectified R/G and Y/B mechanisms.

components of spatial-objectual-chromatic structure—in short, aspects of *coloured form*—rather than colour simpliciter. Recent discussions of representational format have popularised the idea that a single vehicle—paradigmatically, a picture-part or pixel—may represent multiple features, such as shape, size, and colour.[72] A picture-part represents these features *separably*, in the sense that each feature is represented by a categorically different property: shape by shape, size by size, and colour by colour.[73] In population coding models, the related notion is multiplexing, whereby different features are represented by statistically independent properties of the population response, allowing a fixed linear readout of each feature across contexts.

In contrast, filter banks comprise units tuned to combinations of hue × luminance × form, introducing cross-terms and thus covariation between stimulus features. These features are *superposed* rather than multiplexed, with information about different features carried by the very same spikes. As a result, no fixed linear projection can recover pure colour (or pure luminance, orientation, SF) information. Independent readouts for each feature are a decoder achievement, requiring context-dependent projections that account for the ensemble-specific covariations between features. Intuitively, rather than a picture-part carrying separable shape, size, and colour content, we have a glass surface where each ‘pixel’ superposes the scene behind with your reflection and sky glare. To extract the colours in the scene behind, we need a de-mixing strategy at each pixel—one that predicts how those colours covary with the spatial-objectual structure of the scene. Similarly, to extract an object’s colour from a pattern of filter bank activity, we must de-mix the hue × luminance × orientation × SF responses—not via a fixed channel-like projection, but by a context-dependent strategy sensitive to covarying features like edge alignment, boundary ownership, and illumination.

These reformist theses paint a complex picture, but in my view reassuringly so. Nineteenth century enthusiasm for elemental colour sensations was seriously misplaced—and the representational reprise of twentieth century OPT fares no better. If the last forty years has shown us anything, it is that things are much messier than this ‘primitives’ impulse allows. Bit by bit, philosophers have recognised difficulties in accommodating colour phenomena within OPT’s fixed three-dimensional framework, without ever seriously questioning its foundational status. This work drives home the underlying problem: OPT’s

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[72] See Kosslyn et al. (2006), Quilty-Dunn (2016, 2020, 2023), Burge (2018), Davies (2021), Clarke (2022), Block (2023), and Greenberg (2023) for relevant discussion.

[73] Compare Block (2023: 234) on separable versus integral dimensions of an iconic representation.

core commitments are not borne out. Philosophers therefore need new foundations for debates about colour representation, thus colour experience. Cardinal Detection Channels, Topographic Hue Maps, and Filter Banks together provide a suitably variegated alternative, better fitted to the diverse and context-dependent mechanisms by which colour is encoded in early cortex.

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