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LECTURE

The Paton prize lecture 2021: A colourful experience leading to a reassessment of colour vision and its theories

Semir Zeki

University College London, London, UK

Correspondence
Semir Zeki, University College London, Gower Street, London WC1E 6BT, UK.
Email: s.zeki@ucl.ac.uk

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Abstract

In this lecture, given in honour of Sir William Paton, a brilliant scientist and one of Britain's great patrons of biology, I give a personal account of the fundamental issues in colour vision that I have tackled since 1973, when I discovered a cortical zone lying outside the primary visual cortex that is rich in cells with chromatic properties. I do not provide an exhaustive review of colour vision but summarise how my views on colour vision and theories surrounding it have changed in light of that discovery.

KEYWORDS
area V4, colour constancy, colour vision, wavelength and colour

1 | INTRODUCTION

> The trouble with colour vision is the mentality of those that write on it – and of those that read. In most aspects of physiology it is sufficient to offer a fairly plausible and adequate hypothesis; but colour visionaries want nothing less than the truth. The cause of this unreasonable demand lies in this, that whereas nearly all the phenomena of nature are simply observed, those of sensory physiology can also be experienced. [From a Review Lecture by William Rushton (1972) delivered to The Physiological Society in April 1970.]

In the early 1970s, when I was charting physiologically the visual areas of the brain that lie outside the primary visual cortex (area V1) (Figure 1), I encountered a zone rich in cells with chromatic properties (Zeki, 1973); they were located in an area, V4, which I had previously defined anatomically in the macaque monkey (Figure 2) (Zeki, 1971a). This was surprising. At that time, and commonly even today, V1 was considered to be the first and sole recipient of visual signals destined for the cerebral cortex from the retina, through the lateral geniculate nucleus (LGN) (Figure 1). Yet, where colour vision is concerned, there was a mystery about it. Studies on the visual brain in general, and V1 in particular, were dominated by the work of David Hubel and Torsten Wiesel, following their description of the organization of V1 and the preponderance of orientation selective (OS) cells in it. But their description was notable for a conspicuous omission – colour. Where was it encoded? In their 1968 paper on monkey V1, they had written that, although '… in broad outline [its] function is probably now relatively well understood … on the whole the colour responses in [it] have been disappointing' (Hubel & Wiesel, 1968). This was followed by a laconic statement in their Ferrier Lecture of 1972 (Hubel & Wiesel, 1977) that, in V1, 'Colour information is not taken into account at all'. Schiller et al. (1976) had reached similar conclusions from their extensive, computer-based, studies of cells in V1. But others had concluded that a significant percentage of V1 cells had chromatic properties (Dow, 1974), with interesting centre–surround receptive field organizations that made them admirable candidates for processing signals related to colour (Michael, 1978a, 1978b). (The receptive field of a cell is the part of the field of view that, when stimulated, results in a reaction from the cell. A receptive field that has a centre–surround organization is one which is excited by light flashed in the centre of its receptive field and inhibited by light flashed

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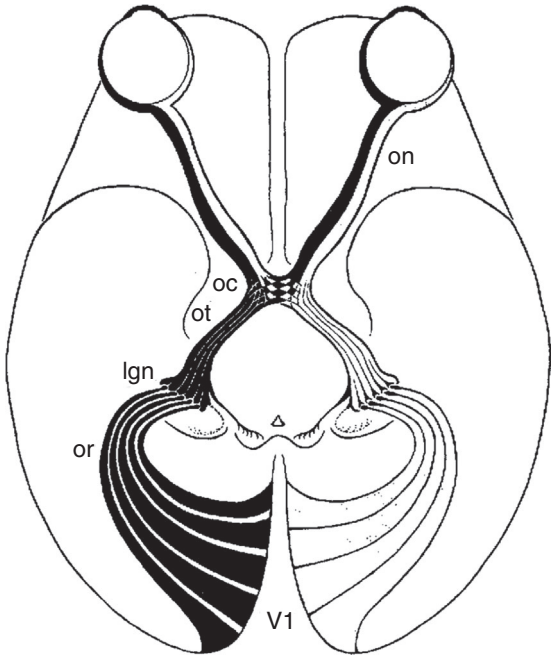

FIGURE 1 The classic diagram showing the projections from retina to cortex. This optic pathway was commonly thought to terminate solely in the primary visual cortex (area V1). For many, even today, area V1 is considered to be the sole entry place of the visual radiation into the cerebral cortex. The projection is retinotopic, with a 'point' in visual space being mapped at a corresponding point in V1. lgn, lateral geniculate nucleus; oc, optic chiasma; on, optic nerve; or, optic radiation; ot, optic tract. (From S. Polyak, *The Vertebrate Visual System*, Chicago University Press, 1957)

in its surrounds. In one of the many variations on this, a cell could be excited by light of one waveband (say, long wave-light) and inhibited by light of another waveband (say middle-wave light) when flashed in its receptive field centre and give the opposite responses to the two wavebands when flashed in the surrounds of its receptive field; such cells are called 'double opponent' cells. There are other variations in which opponent responses are elicited by stimulating different parts of the receptive field.) The extent of V1's involvement in colour vision, if any, was therefore controversial.

Viewed in this light, my discovery in 1973 raised important questions: If V1 was indeed impoverished or lacking in chromatic cells, the question became one of learning the source of their preponderance in V4; if, on the other hand, V1 had a good concentration of such cells, the question would revolve around trying to understand what further processing for colour occurred in V4 and '…why so prominent a group of cells could have been missed by such a prominent pair of investigators [Hubel and Wiesel]' (Livingstone, 2013). Thus, my enquiry into colour vision became part of a more general enquiry into the overall organization of the visual brain. Area V4, Edwin Land's retinex theory (Land, 1974) and the doctrine of functional specialization in the visual brain (Zeki, 1978a) played central roles in this: area V4, because it led me to Land's retinex theory; the retinex theory because it seemed better tailored to understanding the role of area V4 in colour vision; and functional specialization because it was within such a framework that a specialization for colour, with V4 at its centre, was best understood. I therefore begin by a description of V4, followed by a brief description of the retinex theory and the doctrine of functional specialization in the visual brain, adhering as much as I can to a chronological order.

2 | AREA V4, ITS SUB-ORGANIZATION AND PHYSIOLOGY

The position of area V4 in the monkey, and the subdivisions within, are shown in Figure 2. The concentration of wavelength-selective cells is not uniform within it (Zeki, 1983a); there are heavy concentrations posteriorly within V4 and anteriorly within V4α in the macaque, the two together forming the V4 complex (Conway et al., 2007; Tanigawa et al., 2010; Zeki, 1973a, 1983a). I likely initially found high concentrations of wavelength-selective cells within V4 because my early explorations were concentrated in its posterior part; later recordings (Zeki, 1983a) showed that these heavy concentrations are separated from each other by cells which are biased for light of certain wavebands rather than being selective for them (Bushnell & Pasupathy, 2012; Schein & Desimone, 1990; Zeki, 1983a); they are therefore also responsive to white light. More importantly, they also have broad orientational preferences (that is to say, the responses of such cells are not restricted to a small set of oriented lines; they are rather responsive to a broader set of orientations but not to all; hence they are more broad-band orientation selective cells) (Conway et al., 2007; Schein & Desimone, 1990; Zeki, 1983a). This led me and many others since to refer to them loosely as orientation selective (OS) cells, although the OS cells of V4 differ significantly in their orientation tunings from their counterparts in V1, V2, V3, V3A and V3B (Desimone & Schein, 1987; Zeki, 1978b; Zeki et al., 2003), making one wonder whether the term OS cells, indifferently applied, describes them appropriately without adequate qualification. Underlying this common nomenclature is the unstated supposition that all these OS cells subserve the same (form) function, which may or may not turn out to be true, but needs to be tested (see Zeki, 1993a). If the V4 complex is involved in processing signals related to colour and to form in association with colour, then it is possible that the use to which its OS cells are put may be different from the OS cells in other areas, which have other functions. Moreover, unlike the OS cells of V4, those in V1–V3B were not, on the whole, wavelength selective in my studies (Zeki, 1978b). Given this physiological picture, I suggested that two functions attributable to the V4 complex are the processing and the perception of colour and of form in association with colour (Zeki, 1993a).

The wavelength-selective cells in V4 were unlike what had been described before. Not always easy to excite, they commonly had long refractory periods, leading to frustrating waits. They were unresponsive to white light or responded only grudgingly, thus establishing their status as being somehow involved in colour vision, even if they did not always give overt ON and OFF responses to different wavelengths (Schein & Desimone, 1990). Sometimes they would only respond to a particular-coloured cutout (e.g. brown) placed

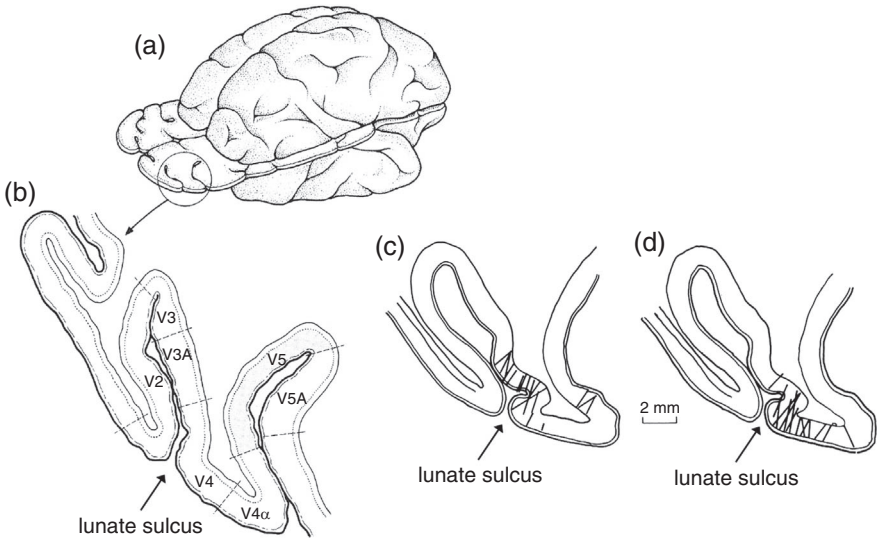

FIGURE 2 (a, b) Diagram illustrating the position of V4 in the monkey brain (a) and a section through it (b). (c, d) The electrode penetrations through V4 that yielded high (average 84 %) (c) and low (average 19%) (d) percentages of wavelength and colour cells, though many of cells encountered in penetrations shown in (d) were wavelength biased in that they gave better responses to light of some wavebands although they were responsive to lights of all wavebands. Tracks from different brains have been superimposed on these sections, and the positions are thus approximate. (From S. Zeki, *Proceedings of the Royal Society B*, 1983; 217: 449–470 and from S. Zeki, *A Vision of the Brain*, Blackwell Scientific, 1993)

within their receptive field – indicating a preference for a dark, rather than light stimulus. Some were later found to be responsive only to isoluminant colour stimuli (Bushnell et al., 2011). V4 cell receptive fields are chromatically even more complex, with the chromatic tuning of subfields within their receptive fields being different from that of the entire receptive field; the consequence is that while the response from the entire receptive field is weak, strong responses can be obtained from sub-regions within it (Nigam et al., 2021). Crucially, most were activated by light of some wavebands but not others; their wavelength sensitivity profiles were variable, with some having the narrowest action spectra (spectral sensitivity curves) I had encountered (Figure 3); this led me to suggest that they may code for specific hues (Zeki, 1980), a suggestion that has since been confirmed by both electrophysiological and human and non-human brain imaging studies (Brouwer & Heeger, 2009; Liu et al., 2020). Within V4, cells registering particular 'colours' seemed to be grouped together, a result that has since been extended significantly (Conway & Tsao, 2009; Kotake et al., 2009; Li et al., 2014; Zeki, 1973a, 1983a). This grouping provided a strong early hint that V4 has a significant role in processing colour. As well, V4 cells had relatively large receptive fields compared to their counterparts in two visual areas that feed it, namely areas V1 and V2 (Cragg, 1969; Zeki, 1969, 1971b), suggesting that its cells may not solely register colour at a 'point'. The physiology of V4 cells is actually more complex than this summary profile would suggest; they have large suppressive surrounds which are only elicitable with stimulation by light of the appropriate wavelength (Desimone et al., 1985). In brief, the responses of V4 cells were not what one might have expected from 'chromatic' cells, given what was known of colour physiology then, a knowledge that had been acquired within a conceptual framework dominated by the theories of trichromacy, and of colour opponency. Their further study thus required a departure from traditional approaches.

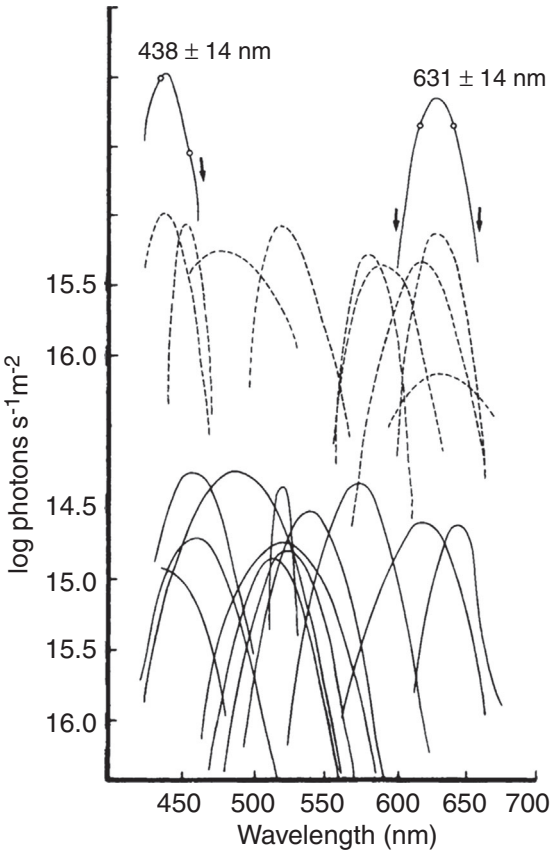

FIGURE 3 Representative action spectra (wavelength selectivities) of V4 cells. Action spectra shown as dashed lines are those of cells inhibited by light at the indicated wavelengths while continuous lines represent the spectra of cells excited by light of the relevant wavelengths. Arrows indicate that no response was obtained at the highest intensities available. (From S. Zeki, *Nature* 1980; 284: 412–418)

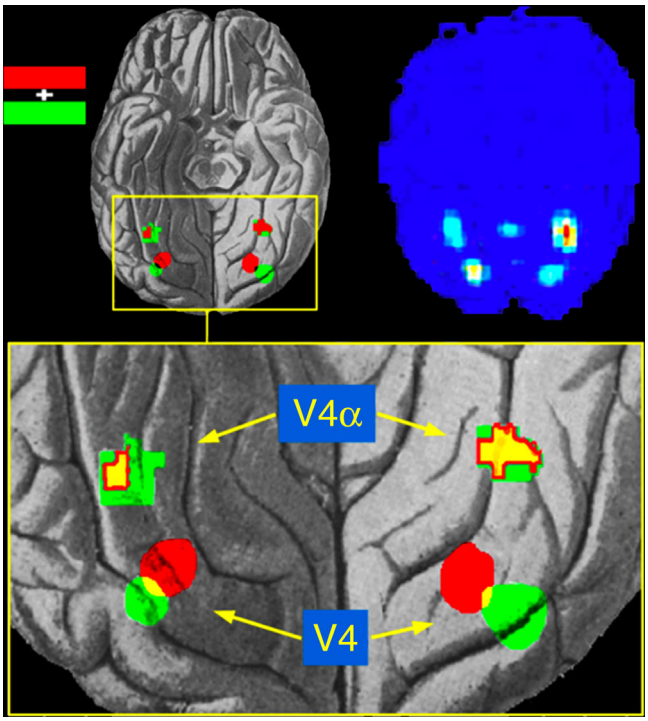

FIGURE 4 Upper two panels: The cortical activity produced in the brain when subjects viewed a multi-coloured Mondrian scene (see Figure 5) in which the wavelength-energy composition of light was changed continuously without changing the perceived colour of the patches. In all three panels the activity shown is on the ventral surface of the brain, within the V4 complex. The cross in the insert in the upper left refers to the fixation point used by subjects when viewing the Mondrian scene. Upper visual fields (and their representation) are shown in red while lower visual fields and their representation are shown in green; the overlap between the two is shown in yellow. The visual fields are represented more topographically in V4 than in V4a (From Bartels and Zeki, *European Journal of Neuroscience*, 2000; 12(1): 172–193)

2.1 | Human V4

My initial conclusions about V4 were derived from physiological studies in the macaque monkey; many advances have since been derived from human brain imaging studies, where V4 has been located in the ventral occipital lobe, within the fusiform gyrus. As in the monkey, it consists of two subdivisions, V4 and V4α, which together constitute the V4 complex (Bartels & Zeki, 2000) (Figure 4). Within this 'complex', visual fields are more precisely mapped topographically within V4 than within V4α (Bartels & Zeki, 2000; McKeefry & Zeki, 1997; Winawer et al., 2010). The former appears to be more concerned with colour and the latter in the processing of coloured objects (Bartels & Zeki, 2000). Wade et al. (2002) have described two regions anterior to V4, which they refer to as VO-1 and VO-2; both, like V4α, are more responsive to colour when associated with objects; the relationship of these two subdivisions to V4α remains obscure.

The ventral shift of the entire V4 complex in the human brain confused those more used to studying the monkey brain, where V4 spans dorso-ventral locations (Figure 2); some found it difficult to understand how both the upper and lower parts of the retina can come to be represented in the lower, ventral, part of the brain in two species separated from each other by some 40 million years of evolution; others saw in it an opportunity to question the existence of a colour centre in the cerebral cortex; Shapley and Hawken (2011) wrote, 'The location of area V4 seems to be quite different in human and monkey cortex'; this led them to argue that V4 is not a colour centre. A good historical account of this issue is given in the review by Winawer and Witthoft (2015). The account is not without its comical side; in trying to resolve this ventral shift, all manner of hypothetical areas, some described as 'orphaned', others as 'improbable' (Kaas, 1993; Zeki, 2003a) and all sitting uneasily in the cerebral cortex, turned up; the descriptions of their positions and relationships to each other, and the representations of the visual fields in them, constitute a dizzying array that is hard to disentangle, digest and understand. The issue is now resolved: both upper and lower visual fields are indeed represented in the ventral part of the human brain, along the fusiform gyrus (Allison et al., 1994; Bartels & Zeki, 2000; Bouvier & Engel, 2006; Goddard et al., 2011; Kennard et al., 1995; Lafer-Sousa et al., 2016; McKeefry & Zeki, 1997; Meadows, 1974; Wade et al., 2002; Wade et al., 2008; Winawer et al., 2010, inter alia).

2.2 | Cerebral achromatopsia

As John Meadows (1974) first pointed out from his analysis of clinico-pathological studies, damage to human V4 leads to the syndrome of acquired cerebral achromatopsia, the most extreme cases of which result in an incapacity to see the world in colour but only in 'dirty shades of grey' (see Zeki, 1990). The presence of a 'centre for the chromatic sense' in the fusiform and lingual gyri, that is to say largely outside V1, had in fact been posited by Louis Verrey (1888), following his studies of a patient rendered hemi-achromatopsic by a unilateral lesion outside V1. This was not to the liking of the two dominant figures in visual brain studies at that time, namely Salomon Henschen and Gordon Holmes. They had charted the position and extent of human V1, which they came to consider as the sole visual centre in the brain (see Zeki, 1990). The presence of a visual centre outside V1, which Verrey's work implied, was a threat to their doctrine; they therefore united in dismissing Verrey's findings forcefully, and the notion of a colour centre outside V1 disappeared from the literature (see Zeki, 1990). This does not seem to have troubled Verrey much; he re-published his 1888 paper in 1930 without any changes, implying that the censorious views of Holmes and Henschen had not led him to change his mind in the slightest (Zeki, 1993b).

In humans, cerebral achromatopsia is variable in its severity. Possibly because of the greater challenge in diagnosing perceptual loss in monkeys compared to humans, where verbal enquiry makes it easier, the effect of cortical lesions, including effects on colour perception, have not been found to be as severe in monkeys. The evidence for achromatopsia from V4 lesions in monkeys is more or less in line with the evidence for akinetopsia (visual motion blindness) in monkeys after lesions in V5, the visual motion centre (Zeki, 1974). Schiller (1993) found that lesions in monkey V4 and V5 produced mild to moderate

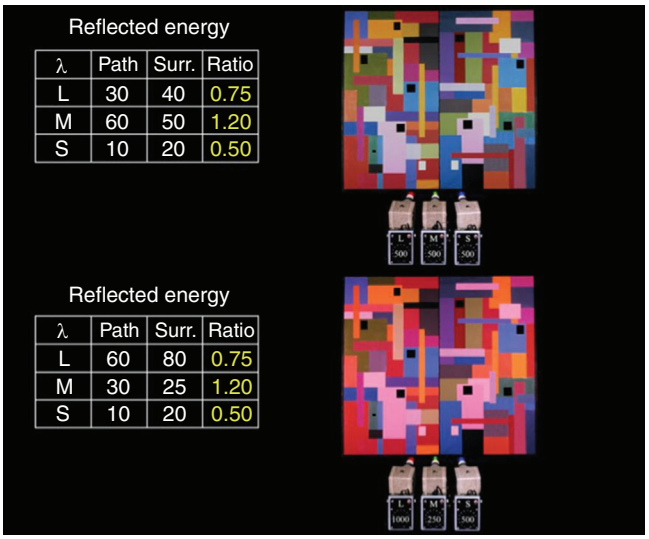

FIGURE 5 The Land retinex experiment. For details see text and Land (1974). During the experiment normal subjects view, successively, different coloured patches of a complex multi-coloured scene (right) illuminated by three projectors, one passing long-wave, another middle-wave and the third short-wave light. Each patch, when looked at (that is, viewed), is made to reflect the identical triplet of energies (see tables to the left). When subjects view different patches successively, each is reported to maintain its colour category despite reflecting the identical wavelength composition of light as patches of another colour, when viewed, reflect. Under these conditions, the ratio of light reflected from the viewed patch and from its surrounds always remains the same (in yellow in the tables). In this figure, the tables to the left give the reflected energies of light of different wavebands reflected from the green rectangle in the lower left (marked with a black spot) for two different viewings. Despite the profound changes in wavelength-energy composition of the light reflected from that rectangle in the two conditions, it is categorized as green, even though its hue changes. Notice that the ratio of light of any waveband reflected from the patch and from its surrounds remains constant throughout (for further details, see text)

defects in colour vision and in motion and flicker perception. Chemical lesions in V5, similarly, produced mild effects from which the monkeys recovered quickly (Newsome & Pare, 1988); the severity of the deficit in motion perception was nothing like that in the akinetopsic human patient of Zihl et al. (1983), in whom the lesions were both bilateral and substantially more extensive than the experimentally restricted lesions placed in monkey cortex. Although relatively mild in comparison to lesions in human V4, monkey V4 lesions have shown a deficit in both constant colour categorization and hue discrimination (Walsh et al., 1992, 1993) from which the monkeys took a longer time to recover – if at all – compared to the time it reportedly took monkeys to recover their capacity for visual motion discrimination after V5 lesions.

3 | THE COMPUTATIONAL APPROACH IN THE RETINEX THEORY

Land's retinex theory (Land, 1974) (see Figure 5) was critical in the development of my views on colour vision. It is a computational theory which proposes that the colour of a surface is determined not only by the wavelength-energy composition of the light reflected from it, but also the wavelength-energy composition of light reflected from its surrounds. The experiments on which it is based are essentially null experiments, in which human subjects view patches of matt paper of different colour, each reflecting a constant amount of light in all directions; the patches are assembled to constitute an abstract scene with no recognisable objects, bearing a superficial resemblance to Mondrian's paintings (Figure 5). The Mondrian scene is illuminated by three projectors, each equipped with a different band-pass filter, one passing long-wave light, one middle-wave light and one short-wave light. The intensity of light coming from each projector can be varied by means of a rheostat and the intensity reflected from any nominated patch can be measured by means of a spectrophotometer (not shown in Figure 5).

In a classic demonstration, the patches of the Mondrian scene are, successively, made to reflect the same triplet of intensities of long-, middle- and short-wave light (the intensities are given in the tables of Figure 5, in milliwatts per steradian per metre square for long-, middle-, and short-wave light, respectively). Naturally, when the wavelength-intensity composition of the light coming from any patch is changed, that coming from its surrounds changes as well, but the ratio between the light of any waveband reflected from a viewed patch and from the sum of its surrounds remains the same (see the tables in Figure 5). When, under these conditions, normal subjects view the different patches successively and each, when viewed, is made to reflect light of the identical wavelength composition, each is reported to maintain its colour category. This led Land to conclude that the perceived colour of a surface is not set solely by the wavelength-energy composition of the light reflected from it alone but depends as well on the wavelength-energy composition of the light coming from the surrounds; more precisely, it depends upon the ratio between the two. By giving equal roles to the two components (a viewed patch and its surrounds), retinex theory departs significantly from more traditional colour theories; my importation of it into physiological studies of colour vision, introducing variations in the experimental details where necessary, was crucial in formulating my views on the causes of functional specialization in the visual brain (Zeki, 1978a).

4 | FUNCTIONAL SPECIALIZATION IN THE VISUAL BRAIN

The discovery, in both monkey and human brain, of a cortical zone rich in chromatic cells and lying outside area V1, within what was then considered to be 'association' cortex, coupled to my discovery of other visual areas in the same 'association' cortex specialised for processing directional motion or form (orientation) (Dubner & Zeki, 1971; Zeki, 1978a, 1978b), led me to the concept of functional specialization in visual cortex and in particular to the separate and parallel processing of colour, visual motion and form (orientation) within it (Zeki, 1976, 1978a, 1978b); this raised doubts about the hierarchical cortical model of visual processing that Hubel and Wiesel (1977), based largely on their studies of OS cells, had promoted. Nor is this functional

specialization restricted to what we may refer to, broadly and perhaps crudely, as primary perception and the processes leading to it. It is projected in time. This follows from psychophysical experiments that show that two visual attributes, presented synchronously in veridical terms, are perceived asynchronously; colour is perceived before form (orientation) by about 40 ms and before directional motion by about 80 ms, thus leading to a perceptual asynchrony in visual perception (Arnold & Clifford, 2002; Linares & López-Moliner, 2006; Moutoussis & Zeki, 1997; Viviani & Aymoz, 2001; Self, 2014). This has implications for understanding the nature of visual consciousness and for addressing the unresolved question of binding, i.e. of how the separately processed visual attributes are combined to give us a holistic picture of our visual world, where colour, form and visual motion are perceived in apparent precise temporal and spatial registration (see Zeki, 2003b, 2020). Finally, functional specialization appears to extend to the formation of concepts related to colour and to visual motion, and probably to other visual attributes as well (Cheadle & Zeki, 2014; Zeki & Stutters, 2013). In summary, functional specialization appears to be a fundamental principle in the organization of the visual brain.

4.1 | The need for functional specialization in the visual brain

The need for functional specialization in visual processing revolves around two crucial facts: first, considering 'visual ecology', events in the visual world do not necessarily co-occur. For example, a red bus moving to the right cannot be defined uniquely by its colour or shape or direction of motion since neither red nor the direction of motion are defining characteristics of buses, which can assume a multitude of different colours and move in a multitude of directions, as indeed can any object. Equally, red can be a characteristic of many different objects, each of which can move, individually or collectively, in any direction. Had the characteristics of redness, of direction of motion and of bus shape always co-occurred, then a bus could be uniquely defined by any one of the three characteristics. But this is not so.

Second, that functional specialization is a computational necessity, reflecting significantly different requirements for processing colour, form and motion – an issue illuminated by asking exactly *how* colour percepts are generated in the brain. To generate colours, the brain has to process signals coming from an object or patch being viewed, and from its surrounds, simultaneously in time (see description of retinex experiments above); the precise configuration of these surrounds and their relationship to the viewed patch is immaterial. On the other hand, all parts constituting a shape must also be processed simultaneously, with the difference that the precise relationship of all parts to each other is now critical. Motion, on the other hand, requires the integration of signals coming from at least two points successively in time. Hence the temporal and spatial computational requirements for processing these different cardinal attributes of vision are sufficiently different for them to necessitate separate processing.

The specialization for colour, form (orientation) and visual motion were the first to be described in the visual brain; since then, many other specializations, including ones for faces (Kanwisher & Yovel, 2006; Sergent et al., 1992), for bodies (Peelen & Downing, 2007) and for objects (Grill-Spector et al., 2001) have been described. No doubt other specializations, and explanations for them, will emerge in the future (see, e.g., Barlow, 1986).

5 | THE 'REPRESENTATION' OF COLOUR IN THE CEREBRAL CORTEX

In addressing the question of a specialization for colour, one cannot disengage from asking the related, cardinal, question of how the brain is organised to register colour. My 1980 paper on colour vision in *Nature*, was entitled 'The representation of colour in the cerebral cortex'. I now regret that title; it reflects an outmoded view about the registration of colour, prevalent at that time and centred around a mistaken belief, namely that the colour of a 'point' in the field of view is determined by the wavelength composition of the light coming from that 'point'. It is a view that supposes that the perception of colour is normally driven mainly by the the physics of light, of which the brain is a passive recipient, simply registering that physical reality. The brain, in brief, was considered to be a spectator rather than an active participant in the generation of colour. A 'point' was, and is, an arbitrary entity; it is imprecisely defined and derived from colour studies using the 'reduction screen' or 'void' mode popular among psychophysicists; in these, the colour of a spot (or 'point') of variable size, viewed in a dark (or achromatic) void, is determined by manipulating the intensities of relatively narrow wavebands of light coming from it or incident on it – a procedure that effectively neutralises the influence of the surround. It is an approach that fails to distinguish between sensation and perception, or rather conflates the two (see below). My experience of the physiology of V4 suggested that this was too simplistic a view, and that perhaps a better way of approaching physiological studies of colour vision was to ask a fresh, and broader, question about the function and role of colour vision and of how it is generated in the brain, rather than merely represented in it; such a question led ineluctably into the world of knowledge and therefore of philosophy.

6 | A PHILOSOPHICAL QUESTION

I was not alone to be surprised by my 1973 discovery of a centre in the visual brain rich in chromatic cells. After presenting my initial results briefly at a meeting of the now defunct Society for Neurobiology, held at St Catherine's College, Oxford, in September 1972, David Hubel remarked, 'You have discovered the philosopher's stone!' It was a prescient comment. Colour constitutes one means of stabilising the world and thus of obtaining constant knowledge of it, in the face of continually changing signals reaching the eye because, in spite of these continual changes in the wavelength composition of light reaching the eye from surfaces, the colour category to which the surfaces are assigned by human observers does not change – a phenomenon commonly, but somewhat inappropriately, referred

to as 'colour constancy'. Colour thus becomes a prime example for illustrating a cardinal philosophical doctrine, common to both Western and Eastern philosophies, namely that the world is never the same from moment to moment and that nothing is permanent except change; to get to the essence of objects and surfaces and learn about their constant properties requires therefore some means of discarding the constant flux in signals reaching us from them, and make these changes ineffectual. Yet both philosophies have also postulated that, underlying this world of constant flux, there is a solid non-changing reality, knowledge of which is more difficult to attain, indeed for Plato and Immanuel Kant almost impossible to do so. What is the unchanging reality in terms of colour vision? Can we ever get to know it, or are we forever condemned not to know the *thing in itself* (Immanuel Kant's *Das Ding an sich*) but to know only the world of appearance? These are philosophical issues, in addition to being physiological problems. The study of colour vision thus provides an admirable setting for addressing physiologically the more general and cardinal philosophical question of how objects and surfaces maintain their identity in spite of the ever-changing conditions in which they are viewed and the ever-changing signals that reach the eye from them – the general problem of stabilising the world in order to obtain constant knowledge of it. Philosophical issues are oftentimes quite remote from the preoccupation of physiologists. Ignoring them so consistently and completely, as almost all physiological studies have done, has been one of the root causes of the confusion regarding colour vision. And by emphasising, whether explicitly or implicitly, a direct relationship between the physics of light at a 'point' and the perceived colour at that 'point', theorists of colour vision have, until only very recently, downgraded significantly, both scientifically and in the popular mind, the direct contribution that the physiological organization of the brain makes to the construction of perceived colour.

7 | SENSATION AND PERCEPTION

Instead of addressing these issues when I started work on colour vision, the well intentioned advice that I received was that I should proceed by studying carefully the principles of colorimetry, Grassman's laws of metameric matches, retinal bleaching, MacAdam ellipses and much else besides, all of which I found not only to be remote from my interests but also very boring, however crucial they may be to studying the contribution of lower levels of the visual pathways to understanding colour vision. Above all, the importance of having a detailed knowledge of the two pillars of colour theory – the Young–Helmholtz trichromatic theory and the Hering opponent colours theory – was impressed upon me. I ended by considering the first not to be a theory of colour vision specifically and the second only partially so. Both are more general theories of vision, including colour but not limited to it. Much of this well intended advice was based on the classical supposition that the colour of a 'point' in the world outside is 'represented' in the brain by registering the wavelength composition of light at that 'point'.

This approach has its roots in the description by Isaac Newton that white light, when passed through a prism, can be broken up into its components, which appear to differ in colour. That white light could be thus decomposed made of this a great experiment in physics; that the components themselves are perceived to differ in colour made of it a great experiment in psychophysics. Newton wrote, 'Every Body reflects the Rays of its own Colour more copiously than the rest, and from their excess and predominance in the reflected Light has its Colour' (Newton, 1704). He added, 'The homogeneal light and rays which appear red, or rather make Objects appear so, I call rubrifick or red-making; those which make Objects appear yellow, green, blue, and violet, I call yellow-making, green-making, blue-making, violet-making, and so of the rest.' These statements imply that the colour of a 'point' in the visual field, say one subtending $1 \times 1°$, will be determined by the wavelength composition of the light reflected from it, the area being red if more long-wave (red) light is reflected from it and green if more middle-wave (green) light is reflected. The 'colour' of that 'point', thus determined, would be registered at a corresponding cortical point (defined as a zone that is 1 mm^2) in the topographically organised area V1, which Henschen had named 'the cortical retina'; he intended, quite literally, to mean a cortical photographic plate onto which an image of the visual world is impressed (see Zeki, 1990), thus leading to the sensation of colour; the colour of adjacent parts of the visual field would be similarly registered in adjacent parts of the topographically organised V1 and so on, a process through which the brain can determine the colour(s) in a visual scene. That was the thinking that was prevalent at that time, often implicitly and sometimes explicitly; it still is prevalent in many quarters today.

But, although Newton linked the perceived colour of a surface directly with the dominant wavelength of the light reflected off it, he added, critically, that:

> … if at any time I speak of light and rays as coloured or endued with Colours, I would be understood to speak not philosophically and properly, but grossly, and accordingly to such conceptions as vulgar People in seeing all these Experiments would be apt to frame. For the rays to speak properly are not coloured. In them there is nothing else than a certain power and disposition to stir up a sensation of this or that Colour.

This important passage serves to separate, perhaps in an oversimplistic way, 'sensation' from 'perception'. I here define sensation as being passive, and leading us to see the colour of a patch as it is determined uniquely by the physical reality. This is not to imply that the visual signals are not processed in the brain, from the retina onwards, by being first converted into electrical signals which are subsequently submitted to a host of interactions, which lead us to see the 'colour' of a point. Perception, on the other hand, is active, the end result of a process in which the brain, besides processing signals, contributes actively to generating what we perceive and applies brain rules or algorithms, in addition to rules derived from the physical world, to do so. Land's experimental paradigm convinced me that the latter was the case and made me want to learn whether the area that I had discovered,

area V4, played a critical role in generating or 'stirring up' the colours that we perceive.

8 | THE TRICHROMATIC THEORY OF COLOUR VISION

Thomas Young qualified Newton's statement when he wrote that, 'now as it is almost impossible to conceive each sensitive point of the retina to contain an infinite number of particles, each capable of vibrating in perfect unison with every possible undulation, it becomes necessary to suppose the number limited, for instance to the three principal colours, red, yellow and blue' (Young, 1802). This statement, commonly regarded as the basis for the trichromatic theory of colour vision, has a grandeur which takes it well beyond colour and includes all of vision, and perhaps much of sensory physiology as well. For it implies that the brain cannot equip its possessor with a receptor for every single colour (which Young equated with wavelength in the passage above) or visual occurrence. It therefore endows receptors with such potential that will allow the organism to have as great a variety of visual experiences as possible. The trichromatic theory of colour vision is perhaps better described as the theory of visual photoreceptors, in that it is the initial stage in a physiological process that enables a wide variety of visual experiences, which include but are not limited to colour vision alone.

Hermann von Helmholtz, who at first only accepted Young's trichromatic theory hesitantly (Hurvich & Jameson, 1949), later drew curves for how he would expect Young's three postulated retinal receptors to respond to light of different wavelengths. He wrote, 'Red light stimulates the red sensitive fibres strongly and the other two weakly, giving the sensation red; green light stimulates the green sensitive fibres strongly and the other two weakly giving the sensation green; blue light stimulates the blue sensitive fibres strongly and the other two weakly, giving the sensation blue' (Helmholtz, 1911). Hence was born the Young–Helmholtz trichromatic theory of colour vision. Note that, as with Young, colour is directly equated with wavelength and, moreover, sensation and perception are treated as one and the same. When Marks et al. (1964) isolated the pigments in the cones of the primate retina and found that there were only three types, each capable of absorbing light from considerable portions of the visible spectrum but each having a maximal absorption sensitivity at a given part (see Figure 6), the remarkable resemblance to what Young and Helmholtz had predicted seemingly made their trichromatic colour theory seemingly secure.

These absorption spectra are very wide (Figure 6); that of the long-wave pigment, for example, extends from about 650 nm to 450 nm; its peak sensitivity is at about 580 nm which, perceptually, falls in the yellow region of the visible spectrum. The consequence is that light of, say, 510 nm, which falls in the green spectral region, will be also absorbed by this pigment if its intensity is strong enough. It is trite to say that such a system cannot account even remotely for colour vision. An answer of sorts is found the principle of univariance (Rushton, 1972), which states that, once a pigment absorbs a photon of light, it no longer distinguishes what part of the visible spectrum that photon

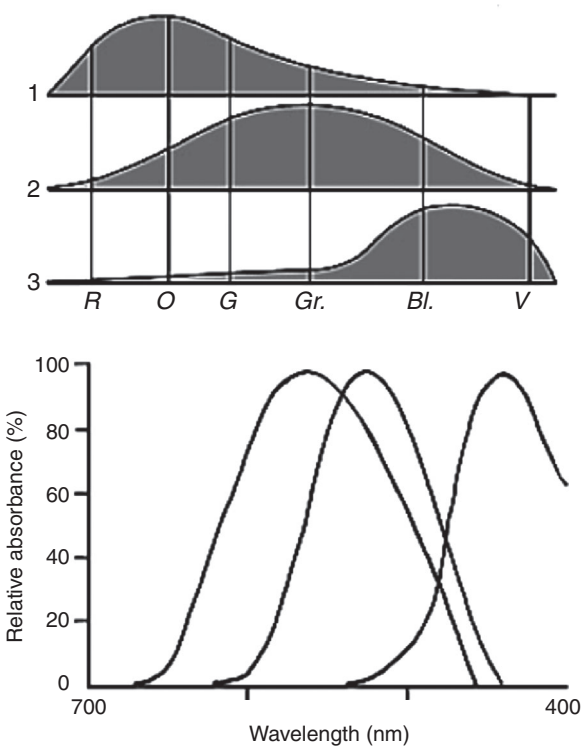

FIGURE 6 Upper part shows the wavelength absorbance spectra of the three retinal receptors (or 'fibres') (1–3) as postulated by Hermann von Helmholtz in his *Handbuch der Physiologischen Optik* (Voss, Hamburg, 1911); the lower part, drawn from the data of Marks et al. (1964), shows the absorption spectra of the three types of cones in the primate retina, as experimentally determined. Bl, blue; G, yellow; Gr, green; O, orange; R, red; V, violet

came from. Colour in such a system is therefore determined, not by the maximal absorbance of the cone pigments but by the ratios of excitation of the three cones receiving signals from a 'point' in the field of view and corresponding to the receptive fields of a small group of cones; Rushton (1972) wrote that our 'sensation' of colour therefore depends '…upon the ratios of these three cone outputs' (Figure 7), an assumption that makes sense in 'void' mode colorimetric wavelength mixing experiments that determine colour at a 'point'. In such an 'excitation-ratio-at-a-point' dependent system the broad spectral curves of the cones no longer present a problem. Whatever its merits, this view cannot be easily accommodated if one goes beyond the colour of a 'point', as determined in reduction screen experiments, to a study of colour in more natural scenes.

The problem with the 'excitation ratio at a point' theory is that changes in the intensities of lights of three wavebands coming from a patch or 'point' isolated from its surrounds ('void mode') modify not only the hue but also the colour category to which the viewed patch is assigned by the observer (see Figure 7). Theories based on 'void-mode' experiments and trichromatic colour theory sidestep the fundamental issue of constant colour categorization – which requires a leap from the 'void' mode to the more natural mode of viewing; they have no way of accounting for the colour category into which a viewed patch is categorised by the observer, unless the 'sensation' of colour

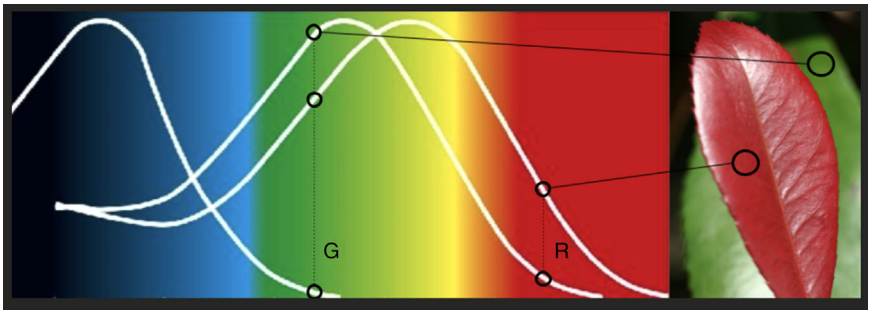

FIGURE 7 The 'excitation ratio at a point' theory to account for colour vision in terms of trichromacy. A 'point' on the red leaf excites both the long- and middle-wave pigments with a ratio between the two excitations that determines the colour. The green 'point' excites all three cones with different ratios, giving the colour green

produced is supplemented by another fundamental operation, which for Helmholtz (1911) was the 'discounting of the illuminant', through the 'unconscious' inference and through the use of judgement and learning, while for Ewald Hering (1877/1964), it was the use of memory colours. The broad-band absorption spectra of the three categories of receptors provide the basis, not specifically for 'representing' colours but for another operation, that of physiological opponency, which narrows the spectral selectivity of subsequent cells in the visual pathways. Spectral sensitivity curves, thus narrowed, can be used for detecting a variety of visual differences, not just colour.

FIGURE 8 Gradations in shade (hue) of green on the surface of leaves. These gradations, and the shapes attached to them, could be registered by cells with different narrow spectral selectivity profiles, without necessarily registering the colour category of the surfaces

9 | THE OPPONENTS COLOURS THEORY OF COLOUR VISION

The opponent colours theory proposes that signals from cones are processed in an antagonistic way, resulting in a sharpening of the spectral sensitivity curves of subsequent cells in the visual pathways and their organization into three opponent channels – 'red–green', 'blue–yellow' and 'black–white', the pairs that cannot live with each other and cannot live without each other. It was first proposed phenomenologically by Hering (1877/1964), who observed that redness and greenness were mutually exclusive qualities of any colour sensation, as were blueness and yellowness. This was later placed on a quantitative, spectral basis by Hurvich and Jameson (1957) and further supported, or so it seemed, by the discovery that retinal circuitry generates cells with so-called opponent properties, excited by one waveband of light and inhibited by another (De Valois, 1960; Svaetichin & MacNichol, 1958). This characteristic of 'cone-subtractive' signal processing has been found from the retina onwards (where a 'cone-subtractive' signal conveys a difference in activation amongst cones of different spectral sensitivity, as opposed to an additive sum of their joint activation). But a problem that has progressively become apparent is that neither the patterns of cone opponency nor the spectral properties of retinal cone opponent mechanisms accord precisely with opponent perceptual phenomena (Zeki et al., 2017). Many studies, however, were quick to label the different physiological classes of cells as 'red–green' or 'blue–yellow' – terms that have persisted to the present day. It follows that neural responses classified in this way are often treated as if their exclusive function is to generate the observed phenomenal colour opponency, but the full causal relationship from one to the other has yet to be uncovered.

The perceptual terminology applied to cone opponent physiology has an additional drawback, in that it tends to mask additional benefits of cone-subtractive signal processing. An undisputed function of physiological opponency is to narrow significantly the spectral profile of post-receptoral cells, compared to the broad absorption spectra of the retinal cones. This results in cells with narrower spectral sensitivity profiles leading to another and more general characteristic – the capacity to detect small differences in reflected wavelength composition between one surface or object and a contiguous one; this capacity can also be used to identify the outline and shape of object surfaces, as opposed to their colour per se (see Figure 8). Cone opponency which generates cells with narrow spectral profiles thus has wider implications than thought and is not necessarily linked to colour vision alone. This part of the opponent colour theory, which is commonly inextricably mixed with the phenomenal colour opponency, is therefore also not specifically a colour theory.

Hence my early beginnings in colour vision were coupled to a serious questioning of whether traditional theories of colour vision are not better described as theories of visual perception in general, rather than those of colour vision. What was needed, at that time, was a theory that addressed colour in a philosophical context, one that would account for the constant colour categorization that is a hallmark of our daily experience of the world of colour.

10 | THE LAND RETINEX THEORY

Into this breach, extending from 1973 to 1978, walked Edwin Land, the legendary American inventor and the only one who, as far as I could tell, had taken constant colour categorization (which he referred to as colour constancy) seriously enough to make it the centrepiece of his research and theory. He had developed a much despised and ridiculed theory of colour vision, the retinex theory (Land, 1974) (described briefly above and illustrated in Figure 5). The contempt in which it was generally held in the world of colour indicated at once that it may contain more than the germs of truth. A flavour of that contempt can be found in this passage from an article by Gordon Walls (1960), entitled, 'Land, Land', which describes the precursor to the retinex theory (Land's two-colour projection demonstrations):

> In effect [Land] says that when he began to use his unorthodox primaries he was not expecting close verisimilitude, and has never strained to attain it, but it is there anyway. It is the fact that he obtains a full series of hues 'from red to blue' when using only red and yellow, or yellow and green (etc.) lights, that must seem the most magical aspect of his results, to those who obtain their scientific information from popular magazines. This degree of verisimilitude secured so cheaply, by such simple means, is what piques the cupidity of those who now contemplate lower costs and higher profits in color photography, color television, and color printing, all as a result of Land's research.

In fact, Land's first papers on the topic were published in the *Proceedings of the National Academy of Sciences* in 1959 (Land, 1959). Continuing this tradition in colour vision, it is worth mentioning here the public glee displayed by old and well liked friends at what they assumed, in 1982, was my discomfiture regarding a specialization for colour (Kelly et al., 1982).

Land asked to see me in July 1978, accompanied by John McCann; his first words were: 'I have known about your work for some time but have waited for it to mature before contacting you.' The lively ensuing discussion continued over lunch, but it was not easy for me to understand his theory without an actual demonstration. Land and McCann decided to go shopping for some suitable coloured papers, to demonstrate as best they could the retinex experimental paradigm.

I was much seduced by the hastily arranged demonstration that they gave me later that afternoon, based on their work (Land, 1974; Land & McCann, 1971). Here was a demonstration that was the basis of a theory which conceived of colour as being generated by a straightforward neural computational process, undertaken somewhere between retina and cortex, hence the term retinex; it was a theory that gave the brain a central role in generating colours, not merely representing them passively. The final product of this computation was the perceived colour; there was no need to postulate that what is seen needs to be supplemented by memory, judgement and learning, as assumed by Helmholtz and Hering. Land did not deny that these factors may play a role in vision; he saw himself, ostensibly at any rate, as only 'going beyond' such extra perceptual formulations. In reality, his theory was a fairly radical departure; it is one that gives judgement, memory and learning a secondary place, assuming it gives them a place at all. Perhaps he was being conciliatory when confronted by so much hostility; perhaps he was being hesitant to claim too much. Whatever the reasons, it was difficult for me to find anyone in the classical colour tradition who was not suspicious of Land's work and the theory attached to his celebrated demonstrations, which some thought he presented with undue ostentation. It is regrettable that there had been no mention or discussion in the physiological literature prior to 1973 of Land's computational approach.

Our discussion continued over drinks that evening, when in the middle of the excitement, Land suddenly proposed that he should fly back to America, prepare high quality displays and return with them and other equipment, to study the responses of single cells in monkey cortex, using his experimental procedure. This placed a huge burden on me, and I explained that physiological experiments often fail. Land was not to be dissuaded; he replied, 'I am a scientist; I know that experiments fail.' I spent a long week trying to ward off failure. Land and McCann returned the following week and came to my lab straight from the airport; we managed to make an early start and were ready to record from cells at noon. To my surprise, and to Land's as well, the first cell that we encountered in V4 was a genuine colour cell, one that responded to a red surface only and not to surfaces of other colour, even when made to reflect light of the same wavelength-energy composition as the red area. The spell of fascination that this precipitated was irreversible.

11 | RETINEX SYSTEM NOT RADICAL ENOUGH

My subsequent, more detailed, study of Land's retinex theory led me to believe that, though powerful, it was not radical enough, being still constrained by past history, especially the trichromatic theory. Since I imported retinex theory and its techniques into colour physiology and into traditional psychophysical studies, it is perhaps useful to outline where I depart from it. Land based his system on three channels, which could be loosely equated with those proposed by Young–Helmholtz; in an effort to mimic as much as possible the wide absorption spectra of the three categories of retinal cones, he chose filters whose transmittance was similarly broad, anywhere between 100 and 200 nm (Land & McCann, 1971). In the retinex theory, the input to the colour computational system in the cortex is, therefore, very broad-band. In fact, Land's perceptual experiments work equally well with much narrower band interference filters, as was common in my physiological experiments (Zeki, 1983b). There is no good reason to suppose that the input to the colour computational system in the primate brain consists of only three broad channels; there could be many more channels, with narrower spectral sensitivity profiles generated by opponent inputs from the retina onwards and with peaks distributed along the entirety of the visible spectrum (Zeki, 1980), especially if the cells of V4 constitute the input channels to the colour computational system.

What we can state with certainty is that more than one channel is needed but how many is not clear. In fact, one can use two filters, one of them arranged to excite the rods at low intensities so that no colour is perceived and the other to excite the cones at over 640 nm so that only the long-wave cone pigment is excited. Use of these two filters to illuminate a Mondrian scene generates a fair gamut of colours (McCann & Benton, 1969).

Land also accepted the opponents theory, writing that 'There is so much reason and logic in these attitudes toward the visual system, that it seems certainly desirable to accept them' (Land, 1964); it is interesting to note that he writes 'towards the visual system' rather than towards 'colour vision' because it is hard to see in what sense the phenomenal opponents colour theory could be incorporated into his retinex theory of colour vision, besides the fact that physiological opponency generates cells with narrow spectral profiles which could input into the colour computational system proposed by Land.

In spite of this, retinex theory remains a very good means of thinking how the brain might achieve colour categorization, once applied to channels processing cone-opponent signals, without worrying too much about incorporating either colour theory into it; it is the most convincing and plausible theory of colour vision that we have, because it gives a central role to colour constancy, thus bringing colour theory closer to the philosophical question of how the brain stabilises the world of colour to obtain constant knowledge of that world. This is why I decided, after 1978, to use its method in my experiments on colour physiology and perception, in a world in which the issue of colour constancy was almost totally ignored (in the pre-1973 literature); where mentioned it was usually regarded as a departure from the norm, the norm being that the colour of a 'point' is determined by the physics of the light at that point. Mausfeld (2003) has given a good summary of this: 'The two authoritative texts in which the then-reigning research perspectives culminated gave colour constancy short shrift: under the heading of chromatic adaptation, they only devoted a few sentences to it (Boynton, 1979, p. 183f.; Wyszecki & Stiles, 1982, p. 440f.)'. He traces this to a tendency for 'Theoretical accounts of colour constancy… in line with elementaristic perspectives on colour perception, to treat variations in the ambient illumination as a kind of "context effect", i.e. as an effect that modifies and distorts the "true" or "original" focal colour, which thus has to be internally restored by compensating processes.' This is because 'The local connection between these "original" colours and colour appearances is considered to be the "normal case" and thus the so-called constancy phenomena are regarded as more surprising and in greater need of explanation than the "normal case".' The root cause for considering constant colour categorization as a departure from the 'norm' is given by Evans (1974) as being due to the 'errors of the application of colorimetric thinking to perception, i.e. inappropriate use of abstractions and concepts that were developed, as refinements of common-sense taxonomies, to serve purposes of colour technology.'

That a departure from the 'norm' was indeed how colour perception and its most important hallmark, constant colour categorization, were regarded can be ascertained by the oft-quoted statements from Herman von Helmholtz and Ewald Hering about how colour constancy is achieved – not through direct 'sensation' but by modifying the 'sensation' through judgement, learning, memory – all of which amount to 'discounting the illuminant' through an 'unconscious inference'. But why 'discount the illuminant' or use 'memory colours' or judgement and learning unless one believes that the colour being perceived under given conditions is not real and needs to be aided by some other, extra direct-perceptual, process or agency? By constantly and approvingly referring to 'discounting the illuminant' and the 'unconscious inference', we have come to believe that these are explanations of how we achieve constant colour categorization; in reality, they are simply alternative, and grander, terms for ignorance. Moreover, it is not even true that the brain 'discounts the illuminant'; rather it very much takes it into account in generating colours (see below). Nor is it true that the brain necessarily uses memory to achieve constant colour categorization. This is not to say that memory does not play a role in colour vision; it clearly does to some variable degree (Bannert & Bartels, 2013; Hansen et al., 2006; Vurro et al., 2013), but its role in constant colour categorization is not as powerful and dominant as the computational brain processes that lead to the generation of constant colour categories. Retinex theory, moreover, does not rely on the commonly used explanation for colour constancy, as the result of adaptation in retinal cells or to 'colour induction', the latter naturally begging the question of how the inducing colours are generated in the first place. I searched far and wide, but in vain, for an alternative approach among the majority who subscribed to these classical views. The eminent biologist Sydney Brenner said to me: 'When you embark on a new field, you should learn a lot about it, but not too much because the many superfluous details will start to distract you from pursuing your main interest.' It is a lesson that everyone, approaching a new scientific area and who does not want to be trapped in the past, as I then was, should heed. I could, after all, have become master of colorimetric methods, only to neglect poorly explored topics in colour vision that were considerably more interesting to me.

12 | CONSTANT COLOUR CATEGORIZATION, NOT COLOUR CONSTANCY

Colour constancy refers to the fact that, while the wavelength composition of light reflected from surfaces changes significantly when they are viewed in different illuminants, the perceived colours of the surfaces change little, if at all. In fact, this is not true, and use of the term without qualification is misleading. For example, when a green surface that is part of a complex scene is viewed in tungsten light, in fluorescent light or in daylight, on a cloudy or sunny day, the wavelength composition of the light reflected from it will vary; with these variations come considerable differences in the hue or shade of green (hue being defined as gradations of colour); it will be a lighter green when reflecting more middle-wave light (in the 500–520 nm range) and a darker green when reflecting more long-wave (in the 600–640 nm range), compared to its surrounds; as well, the hue of a surface changes when the colours of objects surrounding it change. Therefore, the colour of the leaf – its hue – changes with changes in wavelength

composition and in the context in which it is viewed. Yet the colour category to which the leaf belongs (or rather is assigned to by the observer) remains the green one; the hue, but not the colour category, can also change with changes in the surrounds of the green patch (see Olkkonen et al., 2009). This is probably one good reason why artists, among many others, are often sceptical of the term colour constancy; they are puzzled by it, if only because colour to them, and to most others, means shade and hue; artists often strive hard to achieve the right hue of a colour by picking the right surrounds or the right lighting conditions. None, however, is uncomfortable with the designation of constant colour categories. Hence, it is the colour category to which a surface is assigned (by the observer) that is constant and not its hue. I therefore much prefer to break with tradition and speak of constant colour categories and constant colour categorization rather than of colour constancy.

Achieving a constant colour categorization for objects and surfaces is a means by which the brain acquires a constant knowledge about that world. But perhaps there is some constant feature about surfaces in the world itself, something behind appearance, that the brain uses to generate constant colour categories. If so, colour vision becomes one of the most fruitful terrains for learning how the brain registers that constant feature and thus stabilises the world of colour; it may even act as a guide to the mechanisms underlying other stabilizations that it undertakes, because stabilization is the inevitable consequence of trying to establish a perceptual order in conditions of continual change. This edges colour theory closer to the philosophical question of how the brain stabilises the world of colour to obtain knowledge.

13 | THE CONSTANCY BEHIND THE FLUX: COMPARISON OF THE REFLECTANCE OF SURFACES, NOT MIXTURE OF LIGHTS COMING FROM A 'POINT', IS THE DOMINANT OPERATION FOR GENERATING COLOURS

Why did Land's theory attract so much hostility? Partly because he was fond of explaining what was the more dramatic conclusion from his experiments, and one that apparently contradicted a critical statement, made by (Newton, 1704) in his book *Opticks*. To explain how objects and surfaces acquire their colour, Newton had written that, 'Every Body reflects the Rays of its own Colour more copiously than the rest, and from their excess and predominance in the reflected light has its Colour.' Land's experiments led him to conclude that the second part of the sentence quoted above was incorrect. This can be deduced from the experiment illustrated in Figure 5, when the green rectangle is categorised as green in spite of variations in the wavelength-energy composition of light reflected from it (see (Land, 1974; Land, 1985; Newton, 1704). The determining factor, according to Land's theory, was the ratio in wavelength-energy composition of light reflected from a viewed patch and that reflected from the surrounds. This was an unorthodox departure; even with its inadequacies, it led me to an important conclusion: that there is no physical law that dictates that such ratios should be taken; it is instead a brain law and the result is a fundamental step in generating colour by the brain. Colour then becomes a property of the brain, not of the world outside and not of the wavelengths of light which, as electromagnetic radiation, have no colour (Land, 1986).

We can now address the critical philosophical question: is there a constant feature behind the endless change in the wavelength-energy composition of the light reflected from surfaces, which modifies the hues continually, though not the colour categories to which they are assigned by the observer? The answer is 'yes' and that constant property is the reflectance of surfaces for lights of different wavelengths (see Figure 9). Since colour is computed from the spatial ratios of light of the same wavebands coming from perceptually separate patches of uniform coloration (stretching empirically up to 10° in all directions from the patch being viewed (Wachtler et al., 2003) and since reflectance is a constant property of uniform surfaces, the result of the ratio-taking process is the generation of a constant property, namely a constant colour category – or, more simply, colour. Colour is the experience, or the language, that the brain uses to define, within a fraction of a second (Land, 1974), this relationship. There is no need to take judgement, learning and memory into account in order to 'discount the illuminant' because the illuminant is a critical part of what generates the percept; instead of being discounted, it is actually taken into account: the ratio-taking system is probably determined by an inherited brain programme or algorithm that dictates that such ratios should be taken (Zeki & Chén, 2020). Although the details of how that constant ratio is converted into a perceived constant colour category remain unknown, it is through the generation of constant colour categories that the brain stabilises the world of colour. Psychophysical colour matching experiments using Munsell chips to match the nearest resemblance to the Mondrian colour patches show that what is perceived does not vary radically between subjects from diverse backgrounds and cultures; they make the same colour matches when the illuminant in which the Mondrian display is viewed changes; this suggests that the experience of colour is much more objective than is implied in the age old saying *de coloribus non est disputendum* (in matters of colour there is no dispute). This is not to deny that memory, judgement and learning don't play a role, but their roles are not primary ones.

Hence, in the world of colour it is not true that we can never know the *thing in itself* (Kant's *Das ding an sich*); what we do know of the *thing in itself* is its stable spectral reflectance properties. Although many physiologists now accept the importance of reflectance in generating colours, almost none had done so in 1973.

14 | THE CORTICAL SITE FOR THE RATIO-TAKING MECHANISMS

Where in the brain could the centre which, in Newton's words, possesses 'the power and disposition to stir up a sensation of this colour or that' be located? When humans view computer-generated

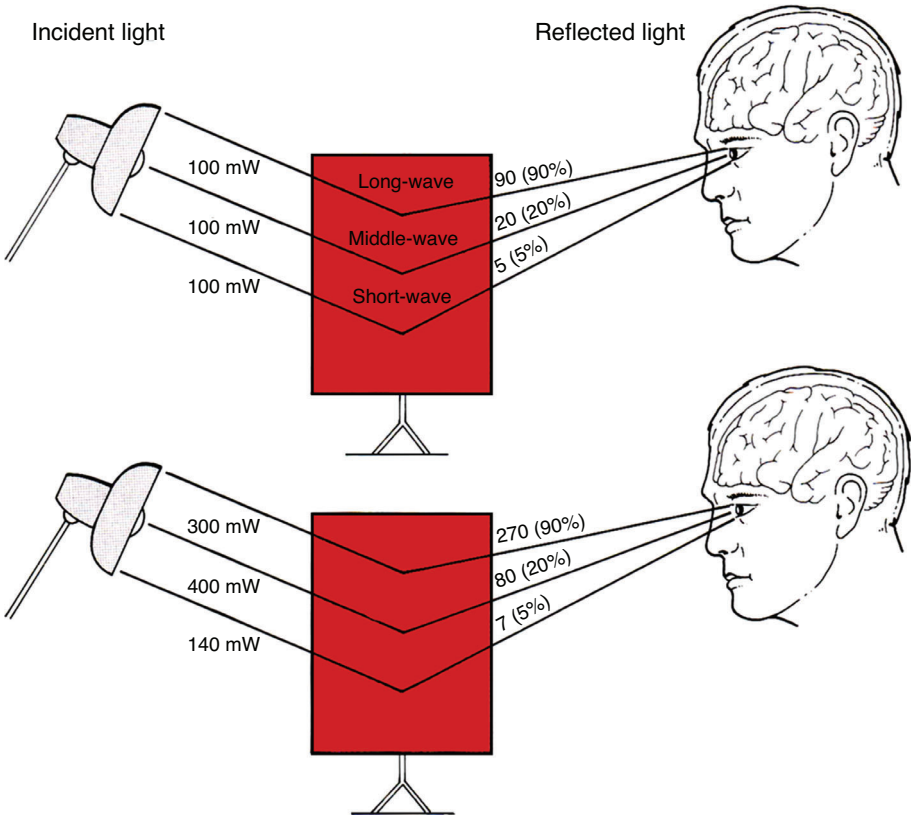

FIGURE 9 Diagram to illustrate the roots of constant colour categorization in colour vision, namely the reflectance of surfaces. In this figure a human observer views a red patch; in the upper part, the light incident on the patch consists of 100 milliwatts (mW) of each long-, middle- and short-wave light. The surface has a high reflectance for long-wave light, in that it reflects 90% of the long-wave light incident on it; it has a relatively low reflectance for middle- and short-wave light, and reflects 20% and 5% of the amounts of these two wavebands incident on it. Thus the amount of long-, middle- and short-wave light reaching the observers is 90, 20 and 5 milliwatts, respectively. In the lower part, the illuminant has changed so that it is now emitting 300, 400 and 140 mW of long-, middle- and short-wave light. Even though the light reaching the eyes of the observer differs from the previous setting, the reflectance of surfaces remains the same and the surface still reflects the same percentage of light as a function of what is incident on it. The reflectance of surrounding surfaces is also constant, and hence the ratio of light in terms of wavelength-energy composition between the viewed patch and its surrounds also remains constant. (From S. Zeki, *A Vision of the Brain*, Blackwell Scientific, 1993)

stimuli in which the wavelength composition of light reflected off a simulated Mondrian display is continuously varied while the patches maintain their correct colour categories, the activity produced in the brain implicates the V4 complex in the fusiform gyrus (Bartels & Zeki, 2000) (see Figure 4). The same is true when natural scenes are viewed under conditions in which the wavelength composition of the illuminant also changes continuously. Thus, at present, the best candidate for the cortical site of the ratio-taking operations and the 'stirring up of the sensation of this colour or that' would seem to be the V4 complex. This is emphatically not to say that V4 acts in isolation, given its reciprocal connections with V1 and V2; both latter areas contain cells that may be important for colour computations; these cells are largely compartmentalised within specific compartments of V1 and V2 while cells with other characteristics are similarly compartmentalised, with projections from different compartments to specific specialised visual areas lying beyond them (DeYoe & Van Essen, 1985; Livingstone & Hubel, 1984; Shipp & Zeki, 1985).

15 | THE SEPARATION OF WAVELENGTH FROM COLOUR IN SINGLE CELL PHYSIOLOGY

A huge problem for understanding colour vision is the result of an inescapable perceptual problem, for both the common human observer and the experimenter; because of it, the latter cannot claim to be the impartial external observer and interpreter of experiments. This is presumably what Rushton (1972), quoted above, was alluding to when he wrote of sensory physiology being 'experienced'. The problem is that different parts of the visible spectrum appear to differ in colour. Light of 610 nm, viewed in isolation in the reduction screen mode looks red, and is categorised as such. But so will a surface that is reflecting light of all wavebands but more light of 610 nm, compared to its surrounds (see Figure 3). This presents a problem for the physiologist. For example, if one were to isolate a wavelength-selective cell, say in V1, and find that it only responds to monochromatic light with a peak at 635 nm and does not respond to white light, one might conclude that it is a 'colour' cell, which signals the colour red (Figure 10). That

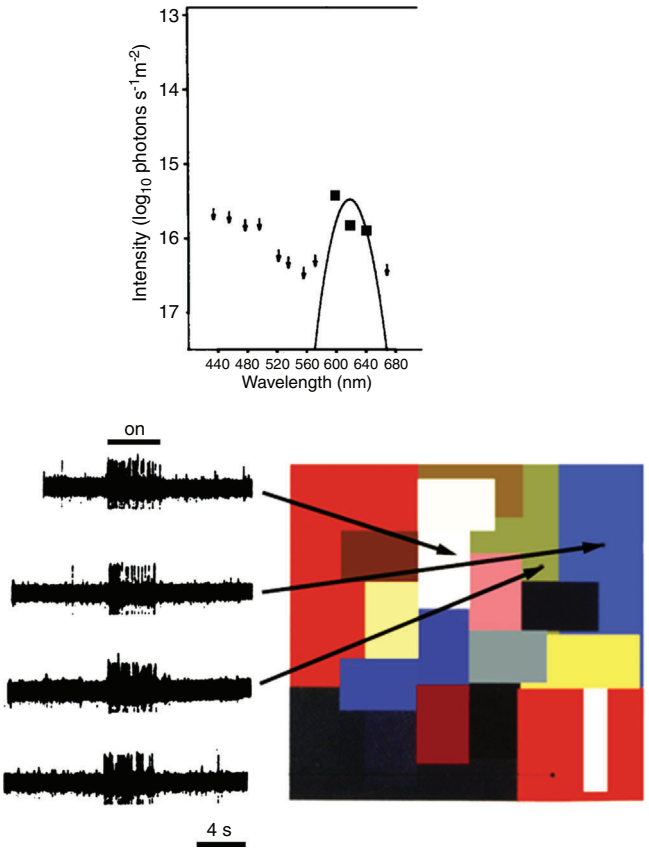

FIGURE 10 The reaction of a V1 cell with a narrow action spectrum peaking in the long end of the spectrum (see inset above) to different patches of a Mondrian display, when each patch was scaled to occupy the receptive field of the cell but was not isolated from its surrounds. When put in the cell's receptive field, each patch was made to reflect the identical triplet of energies, namely 60, 30 and 10 mW sr^{-1} m^{-2} of long-, middle-, and short-wave light, respectively. (From S. Zeki, *Neuroscience* 1983; 9: 741–765)

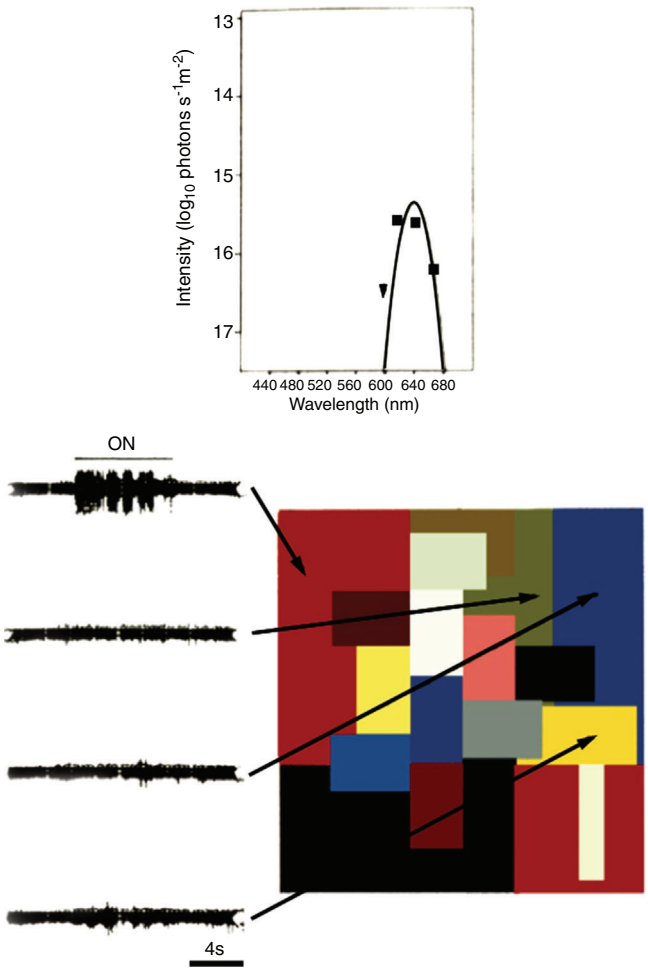

FIGURE 11 The reaction of a spectrally selective cells in V4 (action spectrum in the inset above) to different patches of a Mondrian display. Each patch was scaled to fit the cell's receptive field but was not otherwise isolated from the rest of the Mondrian display. Each patch, when placed in the cell's receptive field, was made to reflect 60, 30 and 10 mW sr^{-1} m^{-2} of long-, middle-, and short-wave light, respectively. (From S. Zeki, *Neuroscience* 1983; 9: 741–765)

that is not necessarily so can be demonstrated by putting different coloured patches of a multicoloured Mondrian display, appropriately scaled, into the cell's receptive field so that the patch remains part of the multi-coloured scene. When a red patch is so placed in the cell's receptive field, and made to reflect a given wavelength composition of light, the cell responds vigorously to it (see legend of Figure 10). When patches of different colour, similarly scaled, are placed in the cell's receptive field and illuminated with light of the same wavelength composition, the cell responds equally vigorously to them, regardless of their perceived colour. In brief, this cell does not distinguish between colours; its response is to the presence of long-wave light with a peak at 635 nm alone – the latter can be ascertained by switching the long-wave light off, when the cell stops responding. Similar responses are obtained from other, similarly narrow-band wavelength-selective cells in both V1 and V2 (Moutoussis & Zeki, 2002; Zeki, 1983b). Hence, in no sense are such cells 'colour' cells, however loosely one may choose to use the term colour.

Such a picture is different from the one presented by a cell in V4 (Figure 11), whose action spectrum is not dissimilar to the wavelength-selective cell of Figure 10. But when tested with patches of different colour which are part of a Mondrian scene, each patch being scaled to fit the cell's receptive field and illuminated with light of the identical wavelength composition, the cell responds only to the red area. The behaviour of this V4 cell, then, is more like one that is signalling a constant colour category and therefore more similar to the human experience of colour. Unlike the V1 cell of Figure 10, this one can more legitimately be called a 'colour' cell. I have only located such cells in V4 but it is possible that similar cells may occur in other areas; although most cells in V1 and V2 are more adequately described as wavelength-selective, weak surround effects which may be a step in the generation of colours have been reported in V1 (Wachtler et al., 2003).

Tests of this kind, to establish that a cell is a 'colour' cell in the sense that its responses correspond to colour perceived by the human (or monkey) observer, impose a considerable burden of proof on the experimenter; there is, however, little way of getting round it if the aim

is to prove that a cell is coding for, or registering, colour rather than merely reacting to differences in wavelength composition. One quick way of screening cells to determine whether they can be accurately labelled 'colour' cells can be found in Moutoussis & Zeki (2002) and Zeki (1983b).

Recordings from single cells in the awake, behaving monkey, concurrent with psychophysical study, confirm that the responses of the cells in V4, or at least some of them, correspond more to perceived colours than to the wavelength properties of the light reflected from the viewed patches (Kusunoki et al., 2006).

Collectively, the results of these experiments speak strongly in favour of separating wavelength – which is electromagnetic radiation and has no colour – from perceived colours. The former constitutes a physical entity, which can provoke a response from cells but the response may not always be related to colour. Perceived colours are different; they constitute an experience that is generated in the brain. I therefore speak of colours as being a construction of the brain (Zeki, 1984).

The long period between the physiological demonstration of the profound difference between wavelength and colour (Zeki, 1983b) and the more recent explicit recognition of this difference (Kim et al., 2020) is worthy of emphasis. In the interval, the common failure to distinguish wavelength from colour, resulting from an adherence to the classical theories of colour vision based on wavelength-discrimination studies, has been continuously perpetuated. The confusion today is apparent in the common usage of terms like 'cone opponent', 'wavelength selective' and 'spectrally selective cells' on the one hand and 'colour cells' 'chromatic cells' and 'colour-opponent' cells on the other, to mean the same thing, without making a distinction between them. There are far too many examples of this, and the following are illustrative ones, however unfair it may seem to detect in the few the fault of the many: 'Signals from blue cones in "red-green" opponent colour ganglion cells of the macaque retina' (De Monasterio, 1979); 'Trichromatic colour opponency in ganglion cells of the rhesus monkey retina' (De Monasterio et al., 1975); and 'Directionally selective response of cells in the middle temporal area (MT) of the macaque monkey to the movement of equiluminous opponent colour stimuli' (Saito et al., 1989).

16 | USES OF NARROW-BAND SPECTRAL SIGNALS GENERATED FROM OPPONENT INPUTS FOR GENERAL VISUAL DETECTION, INCLUDING COLOUR BUT NOT LIMITED TO IT

The cells of area V5, a separate area in the visual cortex, are specialised to signal motion in the field of view, and especially directional motion; they are indifferent to colour (Zeki, 1974) but this does not make them insensitive to using differences in wavelength composition of moving stimuli to detect their direction of motion. If an area not in any way specialised for colour can use wavelength differences in the service of processing what it is specialised for, it is not surprising to find that V5 cells do respond to stimuli of uniform luminance offering only chromatic contrast, although somewhat grudgingly; this was shown by Saito et al. (1989) who wrote that, in V5, 'colour is used for analysis' but conclude, somewhat confusingly though correctly, that the cells of V5 '…do not provide information about the colour of a moving object'. In fact, their stimuli were equiluminant with the background against which they were presented (magenta against cyan) and the polarity did not matter; stimulus and background therefore differed in wavelength composition, a difference that would be perceived by the viewer/experimenter as a difference in colour. Reviewing the work of others who used equiluminant stimuli to activate V5 cells in a paper entitled 'Vision: can colour contribute to motion?', Derrington (2000) asks: 'whether colour patterns that have no luminance variation can evoke the perception of visual motion' and responds by writing that, '…the oldest and the most modern of cognitive neuroscience techniques conclusively dismiss the suggestion that colour signals do not contribute to motion sensation.' In fact, the papers cited in support of this statement are ones in which the wavelength composition was modulated. Statements such as that V5 is '…indeed a principal component of the neuronal substrate for colour-based motion processing' (Derrington, 2000) are inaccurate even when qualified, as in 'directionally selective neurons encode the motion of objects defined by colour while possessing no selectivity for colour per se' (Thiele et al., 2001): there is no evidence that the cells referred to in these statements were 'colour cells' in the sense that I have defined the term above; the cells had never been tested for colour. The confusion here results from the traditional, and enduring, conflation of wavelength and colour. Some may dismiss my insistence on the confusing nomenclature by saying that the term 'colour' is merely a short-hand notation for wavelength: that, of course, is precisely the problem with it.

17 | CAN SINGLE OR DOUBLE-OPPONENT CELLS SIGNAL DIFFERENCES BESIDES COLOUR?

The motion system is not the only one that can exploit differences in wavelength composition to signal what it is specialised for. The form system can do the same but the relationship here is more complicated. Form is an essential part of the colour computational system, in that the difference in wavelength composition of light reflected across the border between two or more different surfaces needs to be computed, and that border has a shape; but it is worth noting that that shape can have any configuration; indeed, one of the features of the colour Mondrian is that it consists of arbitrary but normally rectangular shapes; the stimulus therefore makes the precise formal configuration irrelevant. For shape, on the other hand, the relationship of parts is critical. But whether critical or not, a border signals a transition between adjacent parts that have different characteristics – these characteristics may concern texture, or luminance, or chromaticity. In simpler terms, it is possible to detect the difference between two adjacent, isoluminant surfaces through chromaticity alone.

There is general agreement that single-opponent cells in V1 (i.e. cells with receptive fields showing chromatic but not spatial opponency)

are wavelength but not orientation selective; they may or may not be colour selective; in my experience such cells in V1 and V2 are only wavelength selective whereas they can be colour selective in V4 (Moutoussis & Zeki, 2002; Zeki, 1983b). But there is another type, the double-opponent cell, that many consider to be critical in colour computations; these cells give opponent responses to different wavebands of light in one part of their receptive fields and the opposite opponent responses in another, spatially distinct, part. Several groups have located such cells in V1; they are commonly described as 'colour cells' (see Shapley & Hawken, 2011, inter alia). Some find that most double opponent cells in V1 are also orientation selective, some of them being of the simple and others of the complex variety (Johnson et al., 2008) while others find that most are circularly symmetric (Conway & Livingstone, 2006); yet others find that they are not quite so prominent a group of cells (Ts'o & Gilbert, 1988). Whether orientation selective or not, it has yet to be shown that they are colour selective, in the sense defined here, which is not the same thing as saying that their properties of wavelength differencing may not be used for colour computations. A double opponent cell that is orientation selective could, after all, be well placed to detect the difference in wavelength composition between two adjacent surfaces without signalling the colour of these surfaces. In questioning the modular theory of the organization of the visual brain (Livingstone & Hubel, 1988 and Zeki, 1978a, 1978b), Shapley and Hawken (2011) give a significant role to the 'double-opponent' cells; their properties imply to them that there is no modularity in the brain and no separation between the processing of form and of colour. But where double opponent cells are of the 'complex' type (Johnson et al., 2008), their status as being 'colour' cells becomes questionable. A significant number of the cells studied by Johnson et al. (2004) were in fact double opponent cells of the complex variety. By definition, a complex receptive field does not signal what colour is where within that field; it signals only the presence of a boundary, and the orientation of that boundary. This means that their signals are of no use to higher areas specialised for surface hue identification (Moutoussis, 2015). Since many of these cells also respond to achromatic stimuli of the appropriate orientation, it follows that a cell specialised for detecting edges and lines will use signals from any source, chromatic or achromatic in nature, to do so (often referred to as 'cue invariance'); this does not diminish its specialization for oriented lines but rather enhances it by making more economical use of the sources that enable it to signal orientation (Zeki & Shipp, 1988). There is, in brief, no evidence that these cells are both orientation and 'colour' cells, only that they are orientation-selective cells which can also use differences in wavelength composition to detect orientation. The statement that 'It can be seen that the majority of colour-sensitive cells were orientation selective' (Friedman et al., 2003) is an inaccurate description unless the 'colour' cells had been rigorously tested for colour (see above); it can be rendered more accurate by simple rephrasing, as follows: 'It can be seen that these orientation selective cells can use signals derived from any source, including wavelength differences, to signal orientation'. The difference between the two, apart from the fact that the second one is more accurate in the absence of rigorous testing for colour, is that the first, less accurate, statement can be used to question modularity in the visual brain, as it indeed has (Shapley & Hawken, 2011); the second, more accurate statement cannot be put to such use.

It is the fact that double opponent cells respond differently to different wavebands in different parts of their receptive fields and that these different wavebands are perceived to differ in colour that makes it irresistible to label them as 'colour' cells, as far too many have done. This is one among other reasons why using double opponent cells as an argument against modularity is not convincing, unless one can show that the sole use to which these double opponent cells are put is to 'detect' colour, which is not to say that they may not input into the colour computational system to generate colours. After all, the OS cells of, say, V1, V2, V3 or V3A and B will respond to achromatic stimuli but also to an oriented line that is of any wavelength composition (Zeki, 1978b; Zeki et al., 2003). The argument against modularity based on orientation-selective double opponent cells is not any more convincing than the other argument against modularity used by Shapley and Hawken (2011), that 'there are strong reciprocal synaptic connections between V4 and V5', as if the only reason for areas being inter-connected with one another is to confer their specializations or properties upon one another.

18 | EXTENSION OF THE CONFUSION BETWEEN WAVELENGTH AND COLOUR TO STUDIES OF ACHROMATOPSIA

The confusion between colour and wavelength extends to studies of achromatopsic patients; there are many examples of this. In a classic case, and as with so many physiological papers, the confusion appears in the very title of a paper: 'Complete sparing of high-contrast colour input to motion perception in cortical colour blindness' (Cavanagh et al., 1998). The authors of this paper found it difficult to reconcile the fact that their achromatopsic patient could detect and discriminate high contrast, fast moving colour stimuli, '…equal in all respects to the performance of subjects with normal colour vision'; this leads them to search for a hypothetical cortical site which they locate in a 'dorsal area equivalent to V4…[that might be] a possible site for the strong contribution of colour to low-level motion in these patients and in normal.' In other words, it led them to search for another area in the brain, besides V4 but equivalent to it. But, if one were to accept the dual fact that specialised areas of the brain can tap signals from any source to undertake their function and that wavelength is not the same thing as colour, there would be nothing surprising or unexpected in the demonstration that a person who has lost the ability to perceive colours has not necessarily lost the ability to distinguish stimuli that differ in wavelength composition; nor would there be any need to intuit or search for hypothetical areas that may account for this. It is known, after all, that achromatopsic patients do possess normal cone function (Kennard et al., 1995; Mollon et al., 1980)

19 | 'COLOUR CENTRE' IN THE HUMAN BRAIN

Ever since 1973, I have referred to V4 as the 'colour centre'; I continue to do so. My original reason for so naming it was dictated by the then paucity of cells with narrow spectral properties in the areas that feed V4, namely V1 and V2, coupled to the subsequent knowledge I acquired about a deficit specific to colour perception, the syndrome of acquired cerebral achromatopsia. The picture has changed since and it is now well established that the cells of V1 and V2 code for different visual properties, including chromatic ones, largely in different compartments and distribute their signals selectively to areas of the peristriate visual cortex. I refer to V1 and V2 as 'distributor areas' because they distribute visual signals in an orderly way to the specialised visual areas of the prestriate cortex (Livingstone & Hubel, 1984; DeYoe & Van Essen, 1985; Shipp & Zeki, 1985, 1989; Zeki & Shipp, 1989). Lesions to them lead to total blindness (hemianopias or quadrantinopias, depending on the location of the lesion), including colour vision, if one excepts the residual vision (Riddoch syndrome) that is sometimes the hallmark of lesions in V1 (ffytche & Zeki, 2011; Morland et al., 1999; Zeki & ffytche, 1998, inter alia). That damage to V1 causes total blindness is too well known to be worth documenting in detail here. What is perhaps much less well known is that damage restricted to V2 (and V3) can also result in hemianopia and it is not specific to colour (Horton & Hoyt, 1991). Nor to my knowledge has damage to any other area led to cerebral achromatopsia; at present, the causative lesion is located in the ventral part of the human brain, where the V4 complex is located (Allison et al., 1994; Bartolomeo et al., 2014; Bouvier & Engel, 2006; Meadows, 1974; Wade et al., 2008; Zeki, 1990, inter alia).

Since imaging evidence also shows that, when one reaches to the critical colour-defining experiments described above (Bartels & Zeki, 2000), it is V4 that is principally active, the case for referring to V4 as the 'colour centre' becomes strong. This is not to imply that V4 acts alone in this – its reciprocal connections with the areas that feed it, including above all V1 and V2, and the higher areas to which it projects, including both the inferior temporal cortex beyond TEO and PIT, as well as the parietal cortex, are well documented. V4 has a status that is very similar to V5 in motion processing and perception. No one supposes that V5 acts alone or indeed is the only visual area to undertake motion processing; but there is near unanimous agreement that it is a centre for the processing and perception of visual motion.

I therefore see no present reason for not continuing to refer to the V4 complex, in both the monkey and human brain, as the hub or centre for colour perception.

20 | CONCLUSION

I have naturally given a description of colour vision through the prism of my own work and, for reasons of space, have not been able to cite the many excellent contributions that have been made to the study of colour since 1973. Looking back on the period between 1973 and now, I can only reflect with approval on what William Rushton said in 1972, at the start of his lecture on colour vision to The Physiological Society: 'The trouble with colour vision is the mentality of those that write on it.'

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CONFLICT OF INTEREST

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ORCID

Semir Zeki https://orcid.org/0000-0003-3812-6824

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