radiated by hot, interstellar grains certain limitations can be placed on the size of the emitting region. Assuming the distance is as indicated by a cosmological interpretation of the redshift of $z = 0.089$ with $H_0 = 55$ km s^{-1} Mpc^{-1}, the radius of a 1,500 K blackbody that can generate the observed near IR fluxes is ~ 0.2 pc. If the central UV source has a luminosity of $\sim 10^{12}\,L_\odot$ (see below) and the absorptivity of the grains is neutral between the UV and IR, the grains will reach an equilibrium temperature of 1,500 K at a distance of ~ 0.2 pc from the central source. The IR source must be somewhat larger than either of these estimates, as the bright optical and UV flux from III Zw 2 demonstrates that the source is optically thin (at least towards the Earth) and most plausible dust constituents have greater UV than IR absorptivity, raising the equilibrium temperature for a given distance from the central source. However, the dependences on radius are sufficiently steep that the size should be close to the lower limits estimated above: a size of ~ 0.6 pc would require an optical depth of only 10% and UV absorptivity 16 times that in the IR. A thermally re-radiating source 0.6 pc in radius would smooth out all variations of the UV flux and delay them with a time constant of ~ 2 yr. This estimate agrees well with the brightening of III Zw 2 in the IR in September 1979, ~ 2 yr after the onset of a powerful optical–UV and radio outburst[12]. Further observations in the IR can test this association.

There is already evidence that most Type 2 and those Type 1 Seyfert galaxies with steeply rising IR spectra, such as NGC4151 and NGC5548, emit thermally in the IR[11]. Among Type 1 Seyfert galaxies, III Zw 2 has one of the most slowly rising spectra into the IR. From its behaviour, re-radiation in the IR by dust is an important component of its spectrum also.

The luminosity of the IR source in III Zw 2 is $\sim 4\times10^{11}\,L_\odot$ (ref. 11). From the strength of Hα[13], the luminosity in the Lyman continuum must be $\sim 2\times10^{11}\,L_\odot$. If the nonthermal continuum can be represented by a power law of index -0.4 from 1 μm to the Lyman limit, the luminosity over this spectral range is $\sim 6\times10^{11}\,L_\odot$. Therefore, a significant proportion of the UV continuum of the nonthermal source is absorbed by dust and re-radiated in the IR. The ratio of Hα to IR luminosity for III Zw 2 is among the largest for Seyfert galaxies; for most of these sources the role of dust will be relatively larger than in III Zw 2. From the time scale of the IR variations for all five galaxies we have studied, at least part of this dust lies within 0.1–0.6 pc from the nonthermal sources, depending on the galaxy. The dust therefore lies within or at the outer boundary of the region responsible for the broad emission lines in the Type 1 galaxies.

Table 2 Additional IR photometry

Source	Date (UT)	J	H	K	L	⟨IR⟩	δ⟨IR⟩
III Zw 2	9.10.78	8.6	11.1†	21.4		0.94	0.02
	11.2.78			23.2*		1.04	0.06
	11.19.78	10.8	13.8	23.9		1.08	0.02
	11.12.79	8.9	14.8	28.3	46‡	1.20	0.02
NGC4151	4.24.78	119†	173	231	361	0.97	0.02
	5.22.78		165†	229	392	1.00	0.02
	5.30.78	118†	168	227		0.96	0.02
	6.18.78	126	173†	238		1.00	0.02
	2.9.79	92	124†	166		0.72	0.01
	4.13.79	81‡	104†	136		0.60	0.01
	4.19.79			128		0.56	0.02

Fluxes, aperture, and errors as in Table 1. 0< errors <2% unless otherwise indicated.
* 4% < errors ≤ 6%. † 2% < errors ≤ 4%. ‡ 6% < errors ≤ 10%.

Conclusions

From accurate monitoring of the near IR fluxes of five Seyfert galaxies, we conclude:

Most or all Seyfert galaxies that vary in the optical–UV also vary in the near IR.

The IR variations are not simultaneous with the optical–UV ones, but have the characteristics of dust reradiating the absorbed nuclear UV continuum.

From the time scale of the IR variability, the dust lies near the gas producing the broad emission lines in Type 1 Seyferts.

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The representation of colours in the cerebral cortex

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New insights into how colour is represented in the cerebral cortex and what variables govern the responses of single cortical colour-coded cells have been gained by the discovery of specific visual cortical areas rich in colour-coded cells.

OUR ability to see an almost infinite variety of colours depends on the presence, in the retina, of only a limited number of receptor types. That the number must be limited was first proposed by Thomas Young. He wrote[1], "Now as it is almost impossible to conceive each sensitive point on 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". The identification of three cone pigments in the primate retina[2–5], each with a broad response curve, but each having a maximal sensitivity to a different part of the visible spectrum, was a striking confirmation of Young's theory. In its simplest form, this theory supposed that the colour of each 'point' in the field of view is determined by the relative responses of the three cone pigments at a corresponding 'point' in the retina and that this relative response is determined

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by the amount of light in each waveband coming from that 'point'[6]. Most colour scientists since Young have, however, assigned a role to more central nervous interactions in accounting for colour perception, and especially for colour constancy[7,8]. This refers to the persistence of the colour of objects or of surfaces when viewed in lights of different spectral composition, such as daylight and light produced by a tungsten filament bulb. It cannot be explained in terms of energy–wavelength relationships. Other explanations have therefore been sought and, in most, the cerebral cortex has been given a dominant, but neurophysiologically a vague and ill-defined, role. Helmholtz thought learning and judgement to be critical[6,9]. Hering considered memory to be important[10]. Other factors, such as adaptation, have also been suggested[8]. Land[11,12] in his retinex theory, has sought to explain colour vision (including colour constancy) in computational terms which are essentially independent of energy, surroundings, adaptation, contrast and all psychological factors while being critically dependent on the cortex.

What role, then, does the cortex have in colour perception and how are colours represented there? We decided to explore the responses of single colour-coded cells in the cortex of the rhesus monkey, an animal close to man, with the hope of gaining some insight into these questions.

Wavelength sensitivities of colour-coded cells in the cortex

Anatomical[13,14] and functional [15–17] studies of rhesus monkey prestriate visual cortex have shown that the different areas within it have remarkably different populations of functional cells, thus leading to the theory of functional specialisation in the visual cortex[17,18]. One such specialisation occurs in the fourth visual areas which, unlike other prestriate areas, are rich in colour-coded cells[15–19]. Since the fourth visual areas are the highest cortical areas to which the analysis of colour has been traced, both anatomically[14] and physiologically[16,19], we began by studying the responses and wavelength sensitivities of cells there. Chief among the properties of these areas is the relatively large size of the cells' receptive field[16,19] (when compared to field sizes at equivalent eccentricities in the striate cortex) and the concentration of field positions in the central 20–30° of the retina. One of the most striking features is the absence of a discernible retinotopic organisation such as that found in the striate cortex[20], since field positions in long oblique penetrations move in an unpredictable manner which bears no obvious relation to retinal topography.

Using conventional anatomical and electrophysiological techniques[18], single cells in the fourth visual areas were isolated in the anaesthetised monkey and their receptive fields plotted. Their wavelength response curves (action spectra) were determined by establishing the threshold response at different wavelengths[16]. Figure 1 shows some representative narrow-band action spectra. It is evident that cells in V4 can be selective to narrow parts of the visible spectrum. Just how narrow these are is shown in Fig. 2. This is a plot of peak sensitivity against wavelength. Throughout most of the spectrum, bandwidths range from 10 to 50 nm, with many having a bandwidth at half maximum of between 10 and 20 nm. Thus the response of cells in V4 can be said to approximate more closely what may be termed responses to individual colours, or hues, than anything seen in more antecedent parts of the visual system[21,22].

One can now go further and ask whether cortical colour representation limits the peak sensitivities of cells to certain parts of the visible spectrum, as in the retina. To rephrase Young[1], "is it necessary to limit the peak sensitivities, for instance to the three principal colours, red, yellow and blue". Figure 3 shows the answer to be no. Between them, the peak sensitivities of these narrow band cells cover almost the entire visible spectrum. Superimposed on this wide distribution, however, is a clustering, most cells having their peak sensitivities at 480 nm (blue), 500 nm (green) and 620 nm (orange-red). Hence these are the regions of the spectrum most strongly represented in the cortex. Purple, an extraspectral colour, is also strongly represented. Finally, it is noteworthy that, as in the striate cortex[23], no cells have peak sensitivities in the psychophysically least saturated part of the visible spectrum, that is in the 560–570 nm region[24], roughly where the long-wave pigment has its maximal absorption. Why this should be so is not clear. With further experiments, cells with peak sensitivities in this region may be found. So far, however, it seems that the cortical representation of this part of the spectrum is poor.

Mapping of colours in the cortex

Given such narrow band cells and given the clustering of peak sensitivities in the blue, green, purple and red, it is interesting to ask how these colours are mapped in the cortex. From micro-mapping experiments, there seems little doubt that cells with particular colour preferences are grouped together in the cortex of V4[16,19]. This is especially well seen in perpendicular electrode

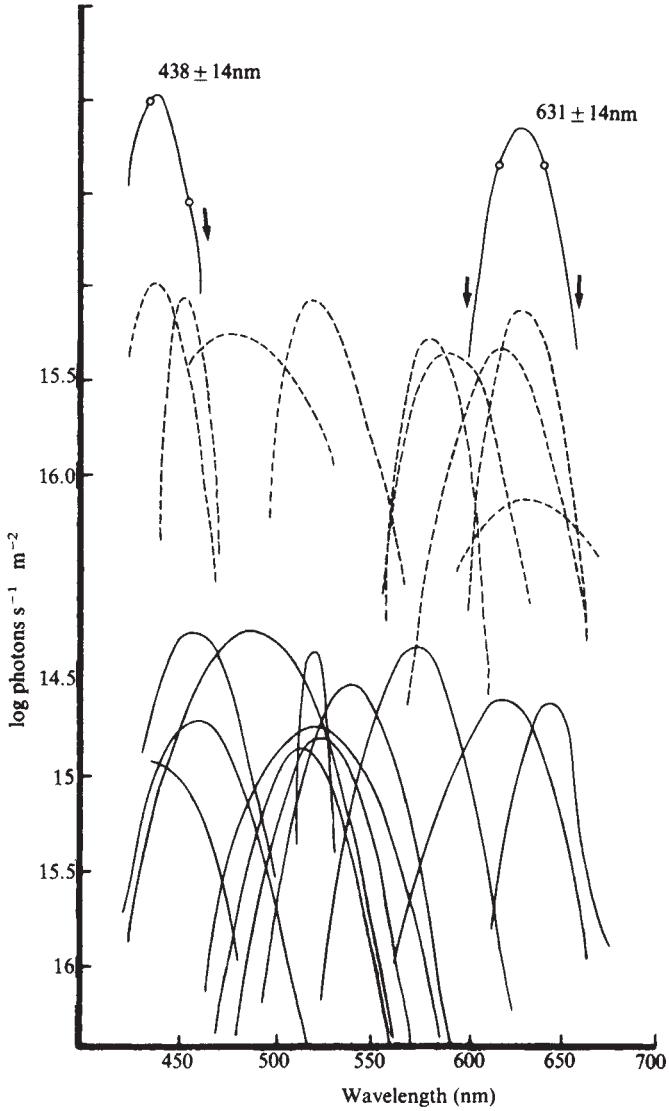

Fig. 1 Representative action spectra (wavelength selectivities) for some narrow-band cells of the fourth visual areas (V4) of monkey cortex. Action spectra were obtained by using neutral density filters and determining the minimum intensity at every wavelength to which there was a response. The upper two spectra show the responses obtained and the manner of drawing the curves to determine peak sensitivity and bandwidth. Arrows indicate there was no response at the highest intensities available. In the conventional way, curves were drawn through the experimental points by using a family of template curves, all of which were parabolas, and judging by eye which one gave the best fit. Action spectra in discontinuous lines are those of cells inhibited by light of the relevant wavelengths, those in continuous lines represent action spectra of cells excited by the relevant wavelengths.

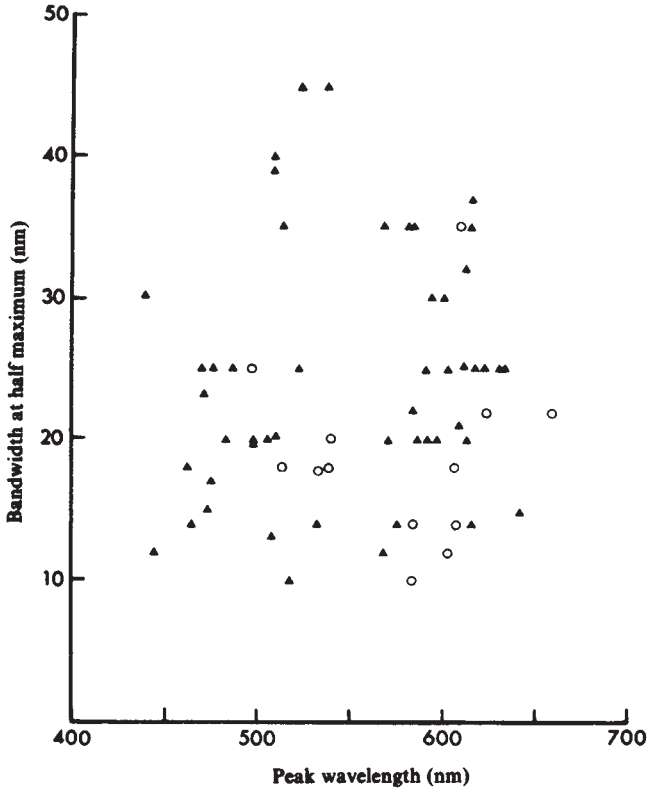

Fig. 2 A plot of peak sensitivity against bandwidth at half the maximum sensitivity for 63 action spectra obtained from 50 cells. ▲, Excitation spectra; ○, inhibitory spectra.

penetrations[16,19]. In oblique penetrations, the changes in colour preferences of successive cells, with electrode distance, are obvious and, in some, such changes are orderly. A fortunate oblique penetration, one of several, is illustrated in Fig. 4. The electrode travelled a total distance of 1,300 μm. Receptive fields of cells were large, and the shift in receptive field position was apparently random. However, the arrangement of cells with respect to one another was far from random functionally. The first three cells responded with an increase of their maintained discharge to blue, and with a decrease to red light. The next five cells were excited by green and inhibited by purple. These were followed by a cell responding to white light only. Finally, the last two cells were excited by red light and inhibited by blue. Action spectra were plotted for most of the cells. It was found that, throughout this progression, peak excitatory sensitivities were displaced from the short to the long end of the spectrum (except for the jump back from the long to the short part from cell 6 to 7). The peak inhibitory sensitivities, by contrast, were displaced in precisely the opposite direction, going through purple, the complementary, to green. Although the peak opponent sensitivities do not all cross at the white point W on the x–y chromaticity chart (Fig. 4) the order apparent when peak sensitivities are plotted on that chart is impressive and suggests that colours may be mapped in an orderly way in the cerebral cortex. The strong representation given to blue, green, purple and red is also evident in this penetration.

A study of the responses of colour-coded cells in the cortex using Land's retinex experiments

The results given above, as well as previous findings[16,19], attest to a high degree of order in the representation of colour in the cerebral cortex: first in generating cells with narrow wavelength selectivities and segregating them into specific cortical areas[17,18], then in mapping the retinal surface in these areas in a manner radically different to the retinal map in other prestriate areas[14], finally in mapping colours in an ordered way. The very segregation of cells sensitive to colour into separate cortical areas suggests that the principles governing the representation of colour in the cortex must be very different from those governing the representation of, say, form or depth. What are these principles?

Edwin Land, the originator of retinex theory, suggested to me that the responses of the cells described above were sufficiently interesting to warrant a new kind of study the purpose of which would be to ascertain the extent to which such responses correspond to, and obey, the rules of colour perception. The simple 'Mondrian' experiments in colour vision[25] were designed by Land to answer the classical question of why colours change so little when the wavelength–energy composition of illumination on objects is changed markedly. By using rectangles of arbitrary shape, size, surround and colour, and by choosing matte papers which reflect a constant amount of light in all directions, he created a multicoloured complex image with no recognisable objects. By illuminating this abstract scene with three bands of wavelengths whose relative energies were variable, he brought into focus the fact that colour sensations are essentially independent of energy and also independent of memory, learning, judgement, surroundings and adaptation. These perceptual experiments were so readily adaptable to electrophysiological ones that it seemed interesting to learn whether there were any cortical cells whose responses would correspond to the sensation of colour produced by the rectangles of the Mondrian display. I am much indebted to Land in the execution of the experiments described below.

Provided with this article are three filters, with cutoff points as follows: short wave, 386 and 493 nm (peak transmittance 432 nm); middle wave, 492 and 580 nm (peak transmittance 528 nm); long wave, 592 nm (peak transmittance greater than 660 nm). Each filter was chosen with a bandwidth such that an observer cannot see variegated colours through it. If one were to view a Mondrian display or a similar multicoloured scene through the red filter one would see a pattern which would be the same in disposition for all three sets of cones, even though the energy available to be absorbed by the middle-wave set and short-wave set of cones will be relatively greatly diminished. Thus all the patches which were variously coloured in unfiltered illumination will be seen as a series of light and dark areas against a reddish wash and the area which was red in unfiltered illumination will be seen as one of the lightest. Other areas such as yellow and white will also appear very light and an observer would not find it possible to predict which, among the areas that appear very light, will be red when the display is later viewed in unfiltered light. For the red area, the transition from this high lightness to a deep red in unfiltered illumination can be better understood by examining the Mondrian again, first through the green filter and after that through the blue filter. For either of these filters, as opposed to the red one, the area which is deep red in unfiltered illumination will be very dark. Thus it is as if the

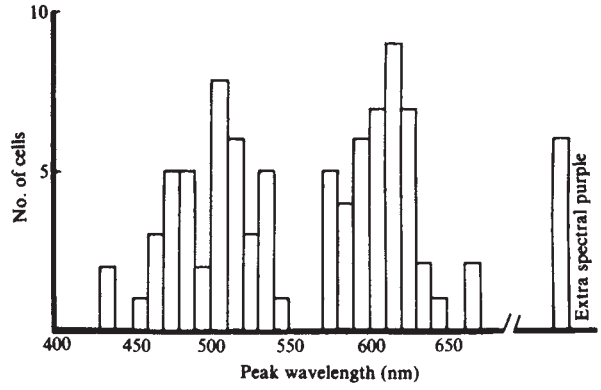

Fig. 3 Histogram of the distribution of peak sensitivities of narrow-band cells in the fourth visual areas (90 spectra obtained from 62 cells).

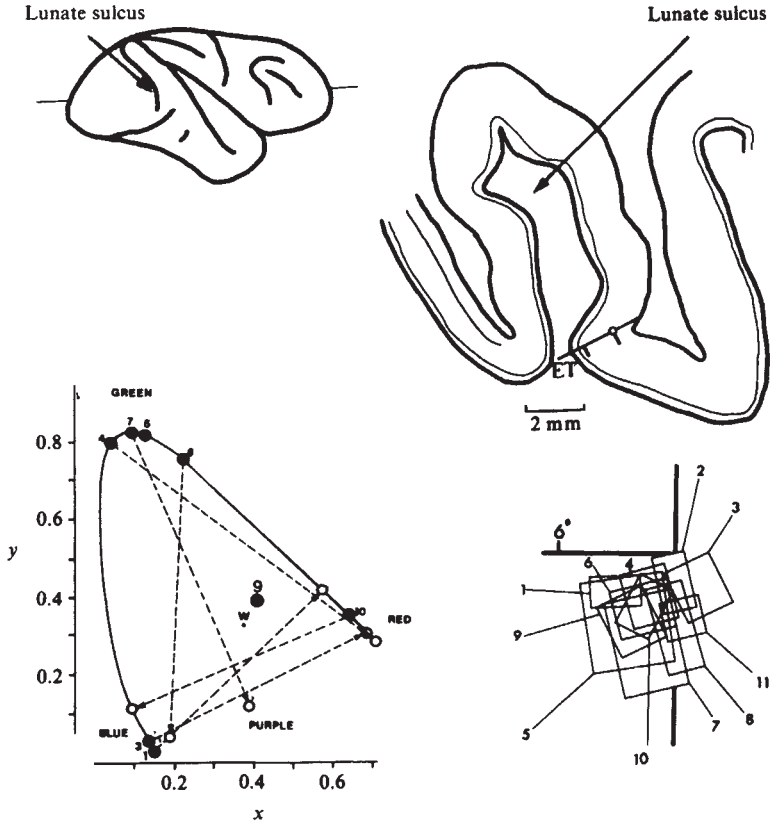

Fig. 4 Reconstruction of an oblique electrode penetration (ET) through the cortex of V4, made at the level indicated on the surface drawing of the brain. Receptive fields of successive cells are shown to the lower right. As in longer penetrations, shifts in receptive field position bear no obvious relation to retinal topography. The peak sensitivities of the narrow-band cells, determined from their action spectra, are entered on the x–y chromaticity chart to the left. The position of cell 9 (white) on the chart was determined from measurements of the spectral distribution of the light source and the spectral reflection coefficients of the screen. ●, Peak excitatory sensitivity; ○, peak inhibitory sensitivity. Cell 5 was lost before the inhibitory part of the action spectrum could be determined.

deep red of the area in unfiltered illumination is the consequence of the simultaneous presence of the high lightness as seen through the red filter and the two low lightnesses as seen through the green and blue filters. In general three completely independent patterns in terms of lightness and darkness will be seen through the three filters respectively. Each of these patterns as seen through one of the coloured filters will not change if a neutral filter of low, medium or rather high density is superimposed on the colour filter. It is this basic phenomenon which manifests itself as colour constancy when the relative flux in the three illuminators is altered (see below). Are there any colour-coded cells in the cortex whose response is similar to the visual experience produced by viewing Mondrian displays in variable illumination?

If to determine a red region within the field of view as being red it is necessary to illuminate the entire scene, not only by long-wave, but by middle- and short-wave light as well (and hence stimulate all three sets of cones over extended retinal regions), it follows that somewhere along the visual pathways colour-coded cells must give their optimal response when a display containing a red region, say, is illuminated not only by long- but by middle- and short-wave light as well. This was studied in the following way. Once the receptive field and the action spectrum of a cell was plotted, a multicoloured Mondrian display was placed on the screen in such a way that for a cell, say, that responded to blue only, a blue part of the Mondrian covered its receptive field. The Mondrian display was made of special matte papers, selected to have a minimum reflectance higher than 10% for any part of the visible spectrum. The display could be illuminated by three projectors, each equipped with a 750-W tungsten filament bulb and with sharp cut band-pass filters, one passing long, one middle and one short waves. The flux from each projector could be set by a rheostat. The illuminating filters were selected by Land to minimise the diversity of colour sensations from the array of coloured papers when only one projector was turned on and, while satisfying the first condition, to transmit as wide a band of wavelengths and as much light as possible[26].

Figure 5 shows the responses of a cell with a narrow action spectrum, responsive to red exclusively. It had no evident opponent input, either in the centre or in the surround. With the Mondrian display in full illumination, it responded only when the red area was put in its receptive field. However, illuminating the display with long-wave light alone (equivalent to viewing it through the red filter) was totally ineffective in activating the cell. It was also unresponsive to illumination with middle- or short-wave light alone. But when all three lights were switched on simultaneously the cell gave a brisk response. This was the very condition in which the area in the cell's receptive field appeared a vivid red to human observers. Hence one's curious impression that the firing of the cell was in fact the sensation of red. In further experiments, identical responses were obtained for cells responding exclusively to green and to blue.

Table 1 Mondrian areas

Cell	White	Grey	Red	Green	Blue	Magenta	Yellow
'Red' cell	–	–	+	–	–	–	–
'White' cell	+	–	–	–	–	–	–
'Green' cell	–	ND	–	I.+ II.+†	–	–	ND
'Red' cell	–	–	+*	–	I.– II.–‡	–	ND

The response of four cells to different areas on the Mondrian display when the energies coming from each area were identical. +, Presence of a response; –, no response. Unless otherwise stated each area of the display was arranged to send 69 milliwatts per steradian per square metre of long-wave light, 31 mW $sr^{-1}m^{-2}$ of middle-wave light and 5 mW $sr^{-1}m^{-2}$ of short-wave light. ND indicates that the area was not studied for that cell.

* There was only 21 mW $sr^{-1}m^{-2}$ of middle-wave and 4 mW $sr^{-1}m^{-2}$ of short-wave light at this reading.

† On a second reading for this cell, energies were arranged so that the area sent 120 mW $sr^{-1}m^{-2}$ of long-wave, 40 mW $sr^{-1}m^{-2}$ of middle-wave and 5 mW $sr^{-1}m^{-2}$ of short-wave light. There was a response.

‡ On a second reading, energies were arranged so that there was 15 mW $sr^{-1}m^{-2}$ of long-wave, 17 mW $sr^{-1}m^{-2}$ of middle-wave and 8 mW $sr^{-1}m^{-1}$ of short-wave light coming from that area. The cell did not respond.

While the responses of the cell illustrated in Fig. 5 are impressively clear, the same basic phenomenon was observed in many other cells, even if the responses were often not as sharp. With all such cells, however, the effects of switching off two of the three projectors, leaving only the one of the cell's preferred colour, was always the same; it led to a dramatic fall in the cell's firing rate. Figure 6 *A–C* shows recordings from groups of cells, all of them responsive to red alone. With the red area of the Mondrian display placed in the receptive field, switching on long wave light alone was ineffective in activating the cells of (*A*), gave a weak response from those of (*B*), and a powerful response from those of (*C*). In the latter, the discharge rate of the cells fell sharply after the initial outburst. Adding the middle- and short-wave lights (which, by themselves, were ineffective in activating the cells) produced the same result for all three groups—a pronounced increase in firing rate. Switching them off also produced the same result—an almost complete cessation of firing.

It is remarkable that for a cell, such as that of Fig. 5, middle- and short-wave lights should, by themselves or in combination, be totally ineffective in activating the cell and yet be instrumental in driving it in the presence of long-wave light—precisely the condition needed for a human observer to experience the sensation of a vivid red in such a multicoloured display. If these cells were themselves comparing the 'lightness records' of that area at the three wavebands, then one might have expected their

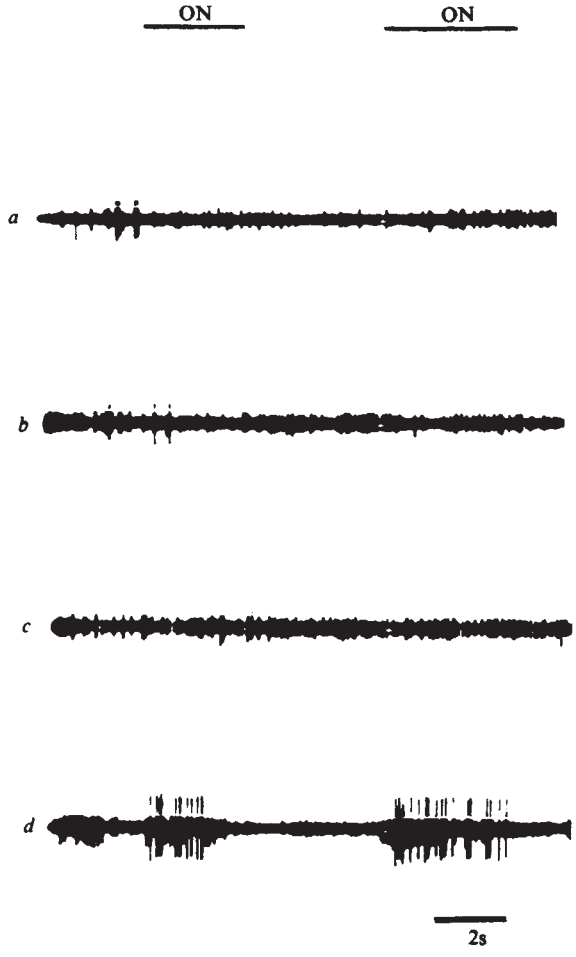

Fig. 5 The responses of a narrow-band red-orange sensitive cell (peak sensitivity 620 nm) to the red area of the Mondrian display when the display was illuminated by *a*, long-wave; *b*, middle-wave and *c*, short-wave light. In *d* the response to illuminating the display with all three projectors simultaneously is shown. To provide long-wave light, a Wratten 29 filter was placed in the light patch. The middle- and short-wave projectors had sharp cut band-pass filters with dominant wavelengths at 525 nm and 440 nm respectively.

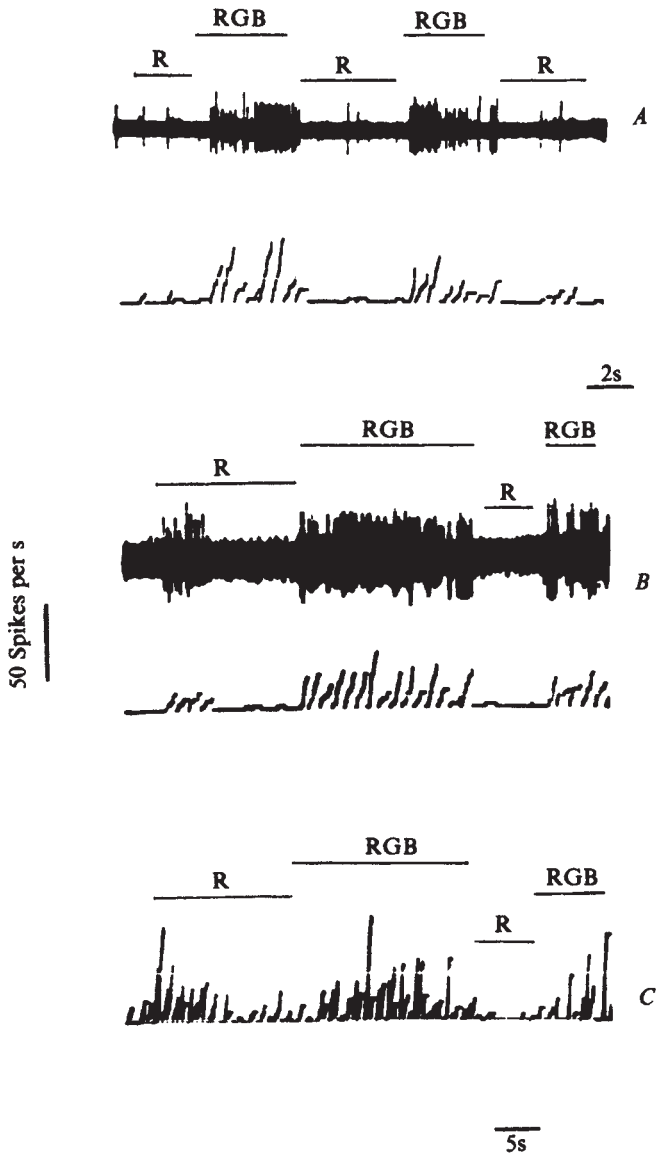

Fig. 6 The responses of three groups (*A*, *B* and *C*) of red-sensitive cells to the red area on the Mondrian display, when the display was illuminated with long-wave light alone (R) and when illuminated with long-, middle- and short-wave light (RGB). In the first two groups, the upper trace is the spike discharge of the cell and the lower trace the frequency of that discharge. For group *C* only the frequency of discharge is shown.

activity to be influenced in some way by light at each waveband. That the burst of activity occurs only when all three projectors are switched on simultaneously suggests that, if such a comparison is indeed the basis of the response, it must occur at antecedent levels. We have no clear notion whether 'lightnesses' at each waveband are registered by individual cells or whether more subtle interactions, requiring the activity of pools of neurones, is needed. It would therefore be premature to hazard a guess as to what level this might occur at. But V4, with the repetitive representation of each region of the retina in it[14,16], is as good a candidate as any. In this context, I emphasise that not all colour-coded cells in V4 behave in this 'experiential' way. Some, with action spectra restricted to the long end of the spectrum, behave much more simply, responding whenever long-wave light is switched on, no matter what part of the Mondrian display is in the receptive field. The role of these cells, and the wiring from them to the ones described above, remain to be established.

If a cell, such as that of Fig. 5, responsive exclusively to the red part of the Mondrian display when the display is trichromatically

illuminated, will nevertheless not respond to it, or do so weakly, when the same display is illuminated by long-wave (red) light alone, it becomes obvious that these responses cannot be dictated by energy–wavelength relationships. But it seemed worth repeating with these cells the experiment that Land reported on human subjects[12]. Specifically, how would the cell of Fig. 5, say, respond if the amount of long-, middle- and short-wave light coming from that area on the Mondrian were made identical to the amounts of those lights coming from another part of the Mondrian, say the white, to which the cell was unresponsive. To do this, the amount of long-, middle- and short-wave lights coming off the white area were read off, one by one, using a Gamma Scientific telephotometer fitted with an equal sensitivity filter[26]. Then, going to the other areas on the Mondrian, the amounts of all three lights were adjusted so that, from each, the identical triplet of energies reached the eye. Table 1 below shows how four narrow band cells behaved when different coloured areas on the Mondrian were made to send identical triplets of energy and put in the cells' receptive fields. It is clear that the responses of these cells could be correlated with colour alone and were independent of flux. For the green cell of Table 1, the green area of the Mondrian display was placed in the receptive field and energies adjusted so that three times more long- than middle-wave light reached the eye from it. The area still appeared green to me, a normal trichromat, and the cell gave a good response. Again, for the red cell of Table 1, the blue area was placed in its receptive field and energies adjusted so that while the area still appeared blue, it nevertheless sent twice as much long and middle, than short wave, light to the eye, and yet the cell still did not respond to it. The independence of these responses from flux is striking.

Figure 7 shows an even more remarkable response, that of a cell responding exclusively to white (of which I have encountered a few examples). When energies were made equal so that each area, when placed in the cell's receptive field, was sending an identical triplet of energies, the cell still responded only to the white area.

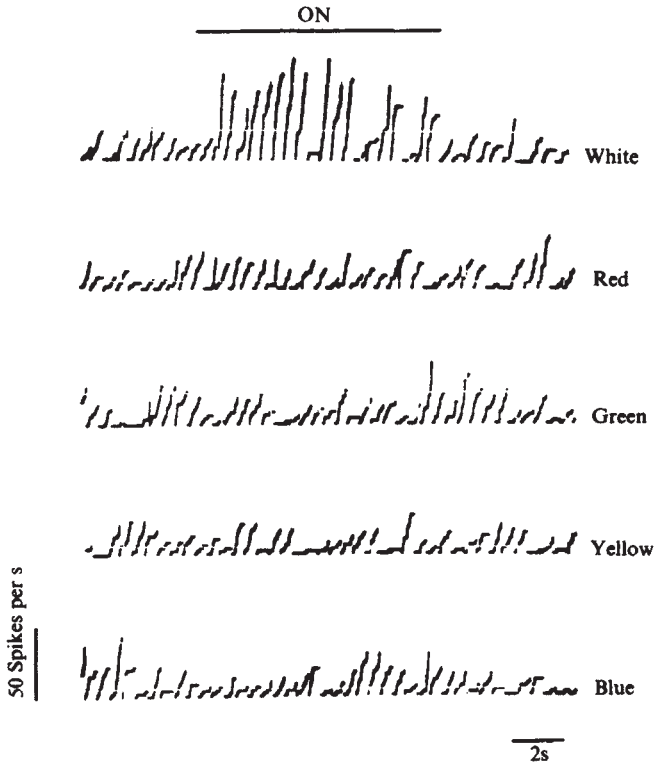

Fig. 7 The response of a cell selective to white when different areas on the Mondrian display were made to send an identical triplet of energies as that coming from the white area and placed in the cell's receptive field.

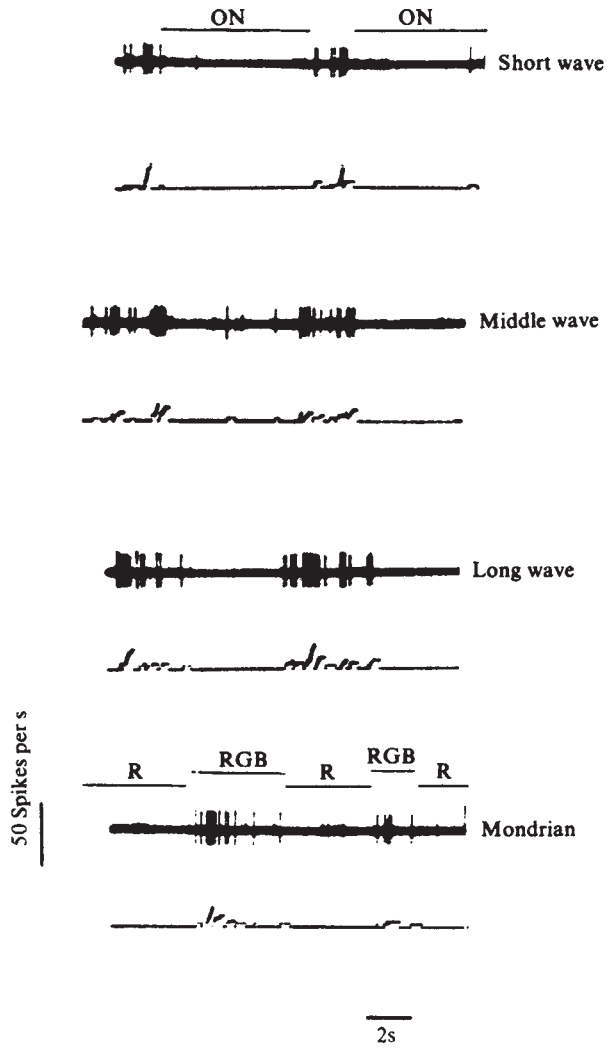

Fig. 8 Upper three traces show the response of a cell to illuminating its receptive field diffusely with short-, middle- and long-wave lights separately. The lower trace shows what happens when the red area of the Mondrian display is placed in the cell's receptive field and the entire display illuminated, first with long-wave light alone (R) and then trichromatically (RGB). The energy from the red area when the display was illuminated with long-wave light alone was 540 mW $sr^{-1}m^{-2}$; when trichromatically illuminated it was 560 mW $sr^{-1}m^{-2}$.

Observations such as these imply that for the single cell, just as for perception, the composition of light in terms of energy–wavelength relationships may be of little importance. Cells specifically responsive to flux, either by increasing or decreasing their firing rate, exist in the prestriate cortex (my unpublished results). However, explaining such responses in terms of energy may be wrong, as the behaviour of the cell of Fig. 8 shows. This V4 cell had a high maintained discharge which was abolished by shining short-, middle- or long-wave light diffusely onto the screen facing the animal. Switching the lights, especially the long wave one, off, led to a vigorous discharge. Superficially, then, the cell behaved as if it decreased its firing rate in response to an increase in flux. But its response using the Mondrian display contradicted this first impression. With the red area of the Mondrian display placed in its receptive field, the entire display was flooded with long-wave light (equivalent to viewing the red area of the display through the red filter). Perceptually, the red area now appeared very light, and the cell's maintained discharge was abolished, as expected. Now, adding short- and middle-wave light to the long-wave (equivalent to viewing the red area of the display[15] in full illumination) and thereby increasing the energy further still led, dramatically, to an

increase in firing rate (Fig. 8). Perceptually, the effect of illuminating the Mondrian display with all three lights was to make the red area appear not only a vivid red, but also darker than it had appeared when the display was illuminated by long-wave light alone. In brief, the responses of the cell could be correlated well with human perception and were dramatically illustrated to be independent of flux.

A new neurophysiology of colour vision

The discovery of specific visual areas rich in colour-coded cells has brought us a step closer to understanding the physiology of colour vision and the nature of colour representation in the cortex. It may also provide a new approach to the study of colour vision. First, functional mapping experiments (see Fig. 4) do not reveal a topographically organised 'map' in relation to the retina. Instead they often show a representation of distinct functions (in this instance, colour) with an arrangement of the cells appropriate to that function and not necessarily following any simple topographic relation to the 'visual field'. No doubt the representation of functions also determines the pattern of anatomical connections of these areas[13,14]. It may therefore be more meaningful to ask for these and other visual areas, how a function is mapped, rather than how the 'visual field' is mapped.

Second, the responses of the cells reported here correspond so well with the sensation of colour that we can now, perhaps for the first time, apply identical techniques for the study of perceptual responses and those of individual cortical cells. Whereas it may be difficult to equate directly the responses of orientation selective cells with the perception of form, or of depth detecting cells with the perception of distance, there is little difficulty in equating the perception of colour with the response of the individual colour-coded cells described here. It seems timely, therefore, to apply the rules of colour perception in natural situations to the study of single cells, although we are, of course, a long way from knowing whether the cells described here are 'experiential' ones, enabling us to see the many and varied colours around us.

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Transforming activity of DNA of chemically transformed and normal cells

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DNA fragments of chemically transformed and normal avian and murine cells induce transformation of NIH 3T3 mouse cells with low efficiencies. High molecular weight DNAs of cells transformed by DNA fragments induce transformation with high efficiencies in secondary transfection assays. It thus seems that endogenous transforming genes of uninfected cells can be activated and efficiently transmitted by transfection. These results are consistent with the hypothesis that normal cells contain genes that are capable of inducing transformation if expressed at abnormal levels.

SUBSTANTIAL evidence indicates that highly oncogenic retroviruses are recombinants between non-transforming viruses and normal cell genes. Examples of transforming viruses that have apparently originated by recombination with different cell genes include avian sarcoma viruses[1–3], avian myelocytomatosis virus[4,5], avian myeloblastosis virus[5], avian erythroblastosis virus[5], Moloney sarcoma virus[6,7], Abelson leukaemia virus[8], Kirsten and Harvey sarcoma viruses[9] and feline sarcoma viruses[10]. In the case of avian sarcoma viruses, it has been demonstrated that genetic information related to the viral transforming gene (*src*) is encoded in the genomes of many vertebrate species[3]. In addition, uninfected avian and mammalian cells contain a normal cell protein ($p60^{src}$) that is closely related to the protein encoded by the avian sarcoma virus *src* gene ($p60^{src}$)[11–13]. The amount of $p60^{src}$ present in avian sarcoma virus-transformed cells seems to be at least 100-fold higher than the amount of $p60^{src}$ present in uninfected cells[11–13]. These observations suggest that viral transformation may result from overproduction of normal cell proteins as a consequence of the insertion of normal cell genes into a viral genome in a manner permitting their efficient expression. If this is the case, it also seems plausible that the transforming genes of retroviruses represent only a subset of the normal cell genes that are potentially capable of inducing transformation if expressed at higher than normal levels. The present experiments indicate that DNAs of both chemically transformed and normal uninfected cells are capable of inducing transformation on transfection. The results thus provide direct support for the hypothesis that potential transforming genes are encoded in the genomes of normal avian and mammalian cells.

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