COLOUR CODING IN THE CEREBRAL CORTEX: THE RESPONSES OF WAVELENGTH-SELECTIVE AND COLOUR-CODED CELLS IN MONKEY VISUAL CORTEX TO CHANGES IN WAVELENGTH COMPOSITION

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Abstract—The reaction of wavelength-selective (WL), wavelength-opponent (WLO) and colour-coded (CO) cells in monkey visual cortex to changes in the wavelength composition of the light reflected from the area in their receptive fields was studied, using multicoloured displays.

Wavelength-selective and wavelength-opponent cells were found to be very sensitive to changes in the wavelength composition of the light reflected from the areas in their receptive fields, irrespective of their perceived natural and void colours. Changes in the wavelength composition of the light reflected from surrounding areas did not affect their responses. They were also sensitive to the order in which lights of various wavelengths illuminated the areas in their receptive fields.

Colour-coded cells were not affected by changes in the wavelength composition nor were they sensitive to the sequence with which the area in their receptive fields was illuminated by lights of different wavelengths. However, they required that the display, with the area of their preferred colour in their receptive fields, be trichromatically illuminated. This and other evidence suggested that such cells were sensitive not only to the illumination of the area in their receptive fields, but of surrounding areas as well.

This evidence reinforces further the distinction between wavelength-selective and colour-coded cells and leads to the conclusion that one function of the wavelength-selective cells must be to register the changes in wavelength composition which occur throughout the day.

The wavelength composition of the light that is incident upon surfaces, and reflected from them, varies continually during the day, a surface now reflecting more light of some wavelengths and now more light of others, depending upon both the illuminant and its relative efficiency for reflecting lights of different wavelengths. Yet the colours of surfaces change very little, or not at all, with such variations. A green surface, for example, remains green whether it is viewed in tungsten or fluorescent light, outside at dawn or at dusk or at midday on a cloudy or sunny day. If one were to measure the wavelength composition of the light that is incident upon, and reflected from, the green surface one would find considerable variations under these different viewing conditions. The fact that the colour of the surface remains green implies that the nervous system must be able, somehow, to discount variations in wavelength composition in assigning colours to surfaces. But it is evident that, to be discounted, these changes must nevertheless be registered. It seemed interesting to ask whether this could be one of the functions of the wavelength-selective (WL) cells described in the first paper of this series. Although selective to lights of certain wavelengths only or responsive antagonistically to lights of different wavelength, these cells respond to a surface of any natural colour if it is made to reflect a sufficient amount of light of their preferred wavelength. The question addressed in this paper is whether such cells are responsive to changes in the wavelength composition of the light reflected from surfaces, whether, for example, a long wavelength selective cell will respond to changes in the amount of long wave light reflected from a surface, relative to light of other wavelengths.

These results were reported briefly elsewhere and the responses of wavelength-selective cells and antagonistic wavelength input cells to changes in wavelength composition recorded on colour video television and demonstrated to the Physiological Society.

EXPERIMENTAL PROCEDURES

Recordings were made from single cells in the visual cortex (V1 and V4 complex) of rhesus and cynomolgus monkeys, anaesthetized with barbiturates and paralyzed with Pavulon. The methods for monitoring the anaesthesia, for refracting the eyes, for plotting action spectra, as well as the general electro-physiological procedures, are described elsewhere. Once a cell was isolated and its action spectrum plotted, its responses to changes in the wavelength composition of the light reflected from an area in its receptive field were studied in the following way. One area of a multicoloured display, similar to the ones used by Land in his perceptual experiments, was placed on its receptive field. The display could be illuminated with three projectors, each equipped with an independent rheostat and with a band pass filter (see Experimental Procedures in the companion paper). The

Abbreviations: CO, colour-coded; WL, wavelength-selective; WLO, wavelength opponent.
display, including the area of it in the cell’s receptive field, could be illuminated with one, two or all three projectors. If the cell was a long wave selective cell, for example, one might begin by putting a red area of the multicoloured display in its receptive field, illuminating the display with long wave light alone, and then adding middle and short wave light. Next, one could start with middle and short wave light alone and then add long wave light. In this way, the wavelength composition of the light reflected both from the area in the cell’s receptive field and from surrounding areas could be changed while at the same time the natural colour of the area in the cell’s receptive field could be monitored. Indeed one reason for using multicoloured displays is that the colour of the areas can be easily monitored by humans as the wavelength composition of the light reflected from them is radically altered. The energies of light of each waveband reflected from any area was measured by means of Gamma Scientific Telephotometer equipped with an equal energy filter and adjusted by means of the three independent rheostats. The area in the cell’s receptive field could be isolated from the rest of the multicoloured display by means of a high quality velvet with a hole in it. The hole could be centred over the area in the cell’s receptive field, thus covering the rest of the multicoloured display.

Between sequences of stimulation, the animal was kept in the dark. That is, with a given area in the cell’s receptive field, the display was illuminated first with light of one waveband, then with light of all three wavebands, then with light of one waveband again. After this, all lights were switched off and the display re-illuminated with a different sequence. The amount of time the animal spent in the dark between stimulations varied but such variations did not affect the cell’s response. Throughout the experiment, the retinal landmarks were periodically checked and the receptive field position of the cell repeatedly checked while it was being studied, by replotting it with monochromatic light of the cell’s preferred wavelength. Such precautions ensured that the areas of the multicoloured display were actually placed on the cell’s receptive field. A cursor was used to place an area of any chosen natural colour on the cell’s receptive field.

Although most of the results were obtained with bandpass filters, on several occasions narrow band interference filters, with bandwidths at half height of 8–10 nm (Ditric Optics Inc.) were used. The results obtained using them were identical to the ones obtained with band pass filters, just as identical results are obtained in Land’s perceptual experiments whether band-pass or interference filters are used.

The nomenclature used in this description is similar to the one used, and defined, elsewhere.

**RESULTS**

One hundred and fifty-nine cells were studied. Of these, 117 were wavelength-selective, responsive to lights of certain wavelengths only (WL cells); 42 gave ON responses to lights of some wavelengths and OFF responses to lights of other wavelengths (WLO cells). The responses from all these cells could be obtained from the receptive fields and there was no evidence of spatial antagonism, except that, for some WL cells, a better response was obtained by restricting the stimulus to the receptive field than by a larger stimulus. Hence, they may have been of the double-opponent variety.8 In addition, the reaction of 34 colour coded (CO) cells from the V4 complex was studied for comparison.

Before describing the responses of wavelength-selective cells in V1 to changes in the wavelength composition of the light reflected from their receptive fields, it is essential to give a brief description of the perceptual effects of illuminating a multi-coloured display with long, middle and short wave light, individually and in combination (Fig. 1). The effects can be easily verified by looking at a multicoloured scene through the long, middle and short wave filters supplied with an earlier article or by looking at a natural multi-coloured scene illuminated with long, middle or short wave light alone.

If the entire display is illuminated with long wave light alone, the whole display acquires a red “wash” to human observers, but one would not be able to predict which of the areas will be a vivid red when the display is later viewed in full illumination. The only difference between the different coloured areas is that some areas appear lighter than others, on a lightness scale that goes from very light to very dark.1, 2 Thus, the red, white and yellow areas of the display will appear very light and barely distinguishable from one another, whereas the green and blue areas will appear dark. When the middle and short wave lights are added (thereby changing the wavelength composition of the light coming from each area), the areas are seen in vivid colours, the red area now becoming red, the green area green and so on. Similarly, if the display is illuminated with middle wave light alone, the entire display will acquire a green wash, and the different coloured areas on the display will acquire different lightnesses, some very light and others very dark. But the lightnesses produced by middle wave light alone will be different from the ones produced by long wave light. Thus, whereas a red area will appear very light when the display is illuminated with long wave light alone, it will appear very dark when illuminated with middle wave light alone (see Fig. 1). Full, vivid colours appear only when the display is illuminated with light of all three wave bands, i.e. with long, middle and short-wave light. Using such a stimulation procedure, then, one can change radically the wavelength composition of the light reflected from any area, while monitoring perceptually the changes in colour of each area.

Figure 2 shows the reaction of a WL cell with a narrow action spectrum (see inset), restricted to long wave (red) light. When a red area of the multicoloured display was placed in its receptive field and the entire display illuminated by long wave light alone, the cell gave a powerful discharge. Under these circumstances the entire display acquired a red wash to human observers, but the red area in the cell’s receptive field, apart from being very light, was not any redder than other areas. Now middle and short wave lights were added to the long wave. The consequence of this was to change the wavelength composition of the light reflected from the red area in the cell’s field as well as from adjacent areas, without changing the amount of long wave light reflected. The area in the cell’s receptive field turned a vivid red to me, but the cell’s response was abolished. Switching the medium and short wave light off (thereby changing the wavelength composition once again) restored the cell’s response. In the next experiment.

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**Fig. 1.** The lightness records of a multicoloured display when it is illuminated with (A) long wave light alone, (B) middle wave light alone, (C) short wave light alone. For details see text.
Fig. 2. The responses of a long wave selective (WL) cell to the red area of the multicoloured display when it was illuminated first with long wave light (L) alone and then middle and short wave light (MS) added (trace A) and when the reverse sequence of illumination was used (trace B). The energies of the long, middle and short wave lights in traces A and B were the same (the standard triplet). When all 3 projectors were switched on (LMS), the red area appeared red to human observers. Inset shows the cell's action spectrum. Receptive field size of the cell was $1' \times 2'$.

Fig. 3. The responses of a long wave selective, colour-coded (CO) cell in the V4 complex to the red area of a multicoloured display. The interrupted line in B shows the position of the receptive field. Note the delay in obtaining the response when all 3 projectors were switched on. The red area in the cell's field was reflecting the standard triplet. Note also that the red area in the cell's receptive field was largely surrounded by white, yellow and green area (i.e. areas which have a high reflectance for middle wave light). The fact that the cell did not give an ON or an OFF response to stimulation with middle and short wave light alone shows that its responses cannot be explained by double opponent inputs. Receptive field size of the cell was $3.5' \times 4'$. Conventions as in previous Figures.
(Fig. 2B) the wavelength composition was changed again, but in reverse order. With the red area of the display still in the cell’s receptive field, the display was first illuminated with the middle and short wave light. There was no reaction from the cell. Now the same amount of long wave light as in 2A was added, and the area in the cell’s receptive field turned a vivid red. But this time the cell gave a brisk discharge. Note that the physical condition of the light reflected from the red surface was identical in the middle part of the upper and lower traces of Fig. 2. But whereas the cell did not respond to the red area when the middle and short wave lights were added to the long wave light, it responded to the identical stimulus when the long wave light was added to the middle and short wave light. In summary, then, although the perception of the natural colour of the area in the cell’s receptive field as red was not dependent on the sequence with which the display was illuminated with light of the three wavebands, the reaction of the long wave (red) light selective cell of area V1 was.

The reaction of this V1 cell was different from that of a colour-coded (CO) cell in the V4 complex which, when stimulated with monochromatic lights, also responded to long wave (red) light only. Figure 3 shows the responses of the CO cell when the red area of a multicoloured display was put in its receptive field. Illumination of the entire display, including the red area in its field, with long wave light alone did not lead to a reaction from the cell. Addition of middle and short wave light, when the red area in the cell’s field turned a vivid red to human observers, resulted in a reaction from the cell. With the reverse sequence, illumination of the display with middle and short wave light did not lead to a reaction from the cell. Addition of long wave light, when the red area again turned a vivid red to human observers, led to a reaction from the cell. In brief, the reaction of this CO cell, unlike that of Fig. 2, correlated with the human perception of red and was independent of the sequence with which the display was illuminated with light of different wavebands.

Returning now to the responses of WL cells, it is important to emphasize that for the cell of Fig. 2, and others like it, the cessation of the response when middle and short wave light were added to long wave light was not due to the adaptation of the cell to long wave light. This is seen in Fig. 4, which shows the responses of a V1 cell with a narrow band action spectrum, restricted to middle wave light. When the green area of the display was placed in its receptive field, this cell gave a powerful discharge when the display was illuminated with middle wave light alone, and the response was abolished by adding long and short wave light (Fig. 4a). Illuminating the display (including the green area in the cell’s receptive field) with long and short wave light alone yielded no response (trace 4b). Adding middle wave light led to a brisk discharge from the cell although it had not responded to the same stimulus in trace 4a. This WL cell, then, behaved much like the cell of Fig. 2, except that it was selective for middle-wave light. Now, if the display was illuminated with middle wave light (Fig. 4c) and the projector left on for a time equivalent to the whole sequence of stimulation in traces 4a and 4b, the cell continued its firing, thus showing that the cessation of the response in trace 4a was not due to habituation. Figure 4d shows, in a sense, the reverse experiment. At the beginning of the recording, middle wave light was switched on, and the cell fired. Now long and short wave lights were added and the cell ceased firing, and continued to remain silent for as long as the long and short wave lights were on (and thus the area in the cell’s receptive field appeared a vivid green). In the last trace (Fig. 4e), the recording was begun with the long and short wave light switched on. There was no response from the cell. Now middle wave light was added, and the cell gave a brisk discharge (when it had not done so to the identical stimulus in trace 4d). This response continued for as long as the stimulus was kept on (with a short break). It is as if the cell “remembered”, at least over a period of 40 s, the sequence with which it had been illuminated. At any rate, it seems quite clear that the response of this WL cell cannot be accounted for by habituation or fatigue. Moreover, when the time course of the stimulation was changed, the reaction of the cell remained the same. That is, if the middle wave light was switched on for 1 s, instead of 10, and then the long and short wave light added, the cell’s response was abolished, exactly as shown in the trace of Fig. 4a. In general, the time over which a middle wave selective WL cell was silent when long and short wave lights were added to middle wave light or a long wave selective WL cell was silent when middle and short wave lights were added to long wave light varied from cell to cell, and varied too with the relative energies of light of the three wavebands. Thus, when with, say, the red area of the display in its field, a long wave selective WL cell responded to illumination of the display with long wave light, the response might be abolished for no more than 1 s when middle and short wave light were added. If so, the period of silence could be increased and even made indefinite by increasing the amount of middle and short wave light. The amount by which middle and short wave light had to be increased, however, varied from cell to cell. This was also true of middle wave selective cells.

Finally, the cell of Fig. 4 reacted in an identical way to areas of different colour, the cell responding when an area of any colour was illuminated with middle wave light alone and its response being abolished by adding the necessary amount of long and short wave light. Since the cell responded to each area when it was illuminated with middle wave light alone, and since areas of different colour acquire different lightnesses in middle wave light, it follows that the responses of the cell did not correlate with the perceived lightnesses.
Here, then, is a V1 cell whose action spectrum might lead one to suspect that it will respond to a green area only, whereas in reality it responds to a variety of different coloured areas under different conditions. The condition determining the presence or absence of a response in the experiments described above was a change in the composition of the light reflected from the area in its receptive field, i.e. either the addition of long or middle wave light. It was shown elsewhere that the actual amount of light of different wavelengths can also determine the responses of these cells, irrespective of the colour of the surface in the cell’s receptive field.

It is important to note that even when WL cells were unresponsive to an area of a given natural colour when it was made to reflect X, Y and Z amounts of long, middle and short wave light they often still responded to changes in the sequences with which the area in their receptive field was illuminated with light of the same energies. Figure 5, for example,
Fig. 5. The responses of a long wave selective (WL) cell in V1 (see inset for its action spectrum), to the blue area of a multicoloured display placed in its receptive field. Illumination of the display with LMS light did not yield a response from the cell, when the energies were the standard triplet (a). However, at these same energies, switching on the middle and short wave projectors first and then adding the long wave one resulted in a discharge from the cell. The reverse sequence of illumination yielded opposite results. When all three projectors were ON (LMS) the area in the cell's receptive field was perceived as blue, yet the cell responded to the blue area in b but not in c. The responses of the cell are shown as its discharge frequency.

shows the response of a long wave selective WL cell to the blue area of a multicoloured display placed in its receptive field. When the blue area was made to reflect 69, 33 and 7 units of long, middle and short wave light and was perceived as a good blue the cell did not respond to it (5a), presumably because there was an insufficient amount of long wave light (at the given energies of middle and short wave light). Yet when the stimulation sequence was changed so that the middle and short wave projectors were turned on first and then the long wave projector, the cell now responded to the blue area. When it did so, the blue area was reflecting 69, 33 and 7 units of long, middle and short wave light and appeared a good blue.
The effect of surrounds

In the experiments described above, the area in the cells' receptive field was part of the multicoloured display. It was obviously important to learn whether the simultaneous illumination of the surround was affecting the responses of these cells, especially since the surround is critical in eliciting responses from cells in the V4 complex and is also critical in determining the natural colour of an area. But the behaviour of WL and WLO cells was the same whether the area in their receptive field was isolated from the rest of the multicoloured display or whether it formed part of it. In the latter context, the precise position of the rest of the multicoloured display, with respect to the part of it in the cell's receptive field, made no difference to the reaction of the cells. This is shown in Fig. 8 for an opponent input cell (WLO), and similar results were obtained for other cells. Here it seems important to emphasize that the responses of these cells did not correlate with perceived void colours, i.e. the colour of an area when it is seen in isolation. For example, examination of Fig. 2 shows that the cell gave a brisk discharge to the red area in its receptive field when its perceived void colour was red and that its response was abolished when the perceived void colour became white. (When a red area is illuminated with the standard triplet and viewed in void, its colour is a light grey or white.) But with a reverse sequence of stimulation, the cell responded when the void colour was white again. This evidence reinforces that presented in the first paper of the series to show that the responses of these cells did not necessarily correlate either with natural or with void colours.

There seems little doubt that, in contrast to the V1 cells described here, the surround is critical in eliciting a response from the CO cells of the V4 complex. But it has been very difficult to determine the extent and the disposition of the critical surround. Examination of Fig. 3 shows an interesting feature about colour-coded cells in V4 that I have often observed. When the red area of the multicoloured display was put in the receptive field of this (long wave selective) CO cell and illuminated with long wave light alone, the cell did not respond. Adding middle and short wave light (when the red area turned a vivid red) led to a response, but only after a delay of about 4 s. The reverse sequence of stimulation also led to a response, but again with a delay. Compared to the almost instantaneous reaction of long wave selective WL cells in V1, this itself suggests indirectly that the cell is responding only after integrating information from large parts of the field of view, not just its

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Fig. 6. The responses of a colour-coded CO cell in the V4 complex to a red area of a multicoloured display when illuminated with long, middle and short wave light (A). B shows the same when the position of the rest of the multicoloured display with respect to the red area in the cell's field was changed.
"receptive field". Such long delays are, of course, difficult to correlate with perception and may be partly due to the fact that anaesthetized preparations were used. But their common occurrence in such cells and absence in wavelength-selective cells seems too important not to be worth mentioning. There is another feature about the responses of the cell of Fig. 3 that is worth noting. The actual position of the rest of the multicoloured display with respect to the red area in the cell's receptive field did not make a difference to the cell's response. When the records of Fig. 3 were obtained, the red area of the display was positioned on the cell's "receptive field" in such a way that, except for a small black patch, the area was surrounded by white, green and yellow areas, i.e. areas which have a high reflectance for middle and long wave light. Yet the fact that this cell did not give either an ON or an OFF response when the display was illuminated with middle and short wave light alone shows that its behaviour cannot be accounted for by supposing it to have double-opponent inputs of the kind found in V1.4

That the position of the surrounds may be critical for eliciting responses from V4 cells is also shown by the responses of the V4 cell of Fig. 6. When tested with monochromatic lights, this CO cell also responded to long wave light only. When a red area of a multicoloured display was placed in its receptive field, illumination with long, middle and short wave light (when the natural colour of the area in the cell's field was perceived as red) resulted in a reaction from the cell. Switching middle and short wave light off virtually abolished the response. [Note that for a long wavelength-selective WL cell in V1 the latter manipulation would have led to an increase in firing (see, e.g. Fig. 2)]. When the same red area was repositioned over the cell's field, but with the rest of the multicoloured display in a different position (trace B), the cell did not respond to the same sequence of illumination as in trace A. This suggests that the surround in trace B was having inhibitory influences, and that these were asymmetrically distributed.

In practice, it was difficult to "dissect out" these surrounds. The difficulty was no doubt due, in part at least, to the probability that these surrounds are themselves complicated. Because of this, the description given above is obviously unsatisfactory in terms of a detailed analysis of surround effects. It is included here only to show how critical the surround can be in determining the response of these cells and to draw further a distinction between these cells and ones which are wavelength-selective.

The responses of opponent input (WLO) cells to changes in wavelength composition

The responses of a narrow band WLO cell with an ON response to long wave light and an OFF response to middle wave light are shown in Fig. 7 (see inset of Fig. 7 for its action spectrum). The ON and OFF responses were obtained from the same part of the receptive field. Stimulation of the receptive field with a small spot of light, the size of the field, or with a large spot going well beyond the receptive field, yielded identical responses. Yet when a red area of the multicoloured display was placed in its receptive field and the display alternately illuminated with long wave light and then trichromatically, followed by a reverse order of illumination, the responses of this opponent input cell hardly differed from that of the cell of Fig. 2 whose action spectrum did not reveal an opponent, inhibitory input.

Fig. 7. The responses of an opponent input (WLO) cell in V1 to a red area of a multicoloured display placed in its receptive field. Inset shows its action spectrum where the triangles indicate OFF responses and the crosses ON responses. Conventions as in previous Figures.

How would an opponent input cell react if one were to put areas of different natural colour in its receptive field and repeat the experiments described above? Figure 8 shows the responses of a middle wave ON, long wave OFF cell to areas of different colour, either when they were part of a multicoloured display or when they were isolated from the rest of the display. When a red area was placed in the cell's receptive field and the display illuminated with middle wave light alone, the cell gave a brisk discharge. Adding long and short wave light abolished the response; switching them off restored it. Illuminating the display in reverse order, gave the opposite results.
Fig. 8. The responses of an opponent input (WLO) cell in V1 to areas of different colour from a multicoloured display. In I, the responses were obtained when the areas in the cell's receptive field formed part of the multicoloured display; in II, when they were isolated from the rest of the display. Traces A show the responses of the cell when a green area of the display was placed in its receptive field and the display illuminated first with middle wave light and then with all three projectors. Traces B show the responses of the cell to the reverse order of stimulation, i.e. with long and short wave light first, followed by light of all three wavebands. Traces C and D were the responses of the cell to the identical sequence of illumination when a red area of the display was placed in its receptive field. Traces E, F show the responses to the same sequence of illumination when a white area of the display was placed in its receptive field. Conventions as in previous Figures.

just as with the green area. In other words, the cell was unresponsive when the long and short wave lights were switched on and gave a brisk discharge when the middle wave light was added, in spite of the fact that moments before it had not responded to the identical stimulus. The reaction of this cell to the blue and white areas was identical to what has been described above. It is important to note that the response of the cell was the same whether the red or green area was placed in the receptive field. When a red area in a multicoloured display is illuminated with middle wave light alone it appears perceptually very dark; when a green area is illuminated with middle wave light alone it appears light. Hence the response of this opponent input cell was to wavelength alone and independent of the apparent lightness.

Like the responses of the WL cells described above, there was a cell to cell variation in the relative amounts of lights of different wavebands which, when added to one another, resulted in an activation or an inhibition of the cell. Thus one middle wave ON, long wave OFF cell responded when, say, a green area placed in its receptive field was illuminated with 50 units of middle wave and its response abolished by the addition of 40 units of long wave and 10 units of short wave light. But the response of another, similar, cell to illumination of a green area in its receptive field with 50 units of middle wave light could only be abolished by the addition of 70 units of long and 10 units of short wave light.

In summary, the wavelength-selective cells, as well as the opponent wavelength input cells, described here were found to be sensitive to changes in the wavelength composition of the light reflected from an area, independently of its colour.

The experiments described above show that the WL cells of V1 react to changes in the wavelength composition of the light reflected from a surface, regardless of its natural colour, although one could not have predicted this by simply examining their action spectra. In fact, there are cells in V1 whose
with long wave (red) light alone, and then switching to middle wave (green) light, yielded a powerful discharge from the cell, whereas the reverse order of stimulation was ineffective. Thus if one had stimulated with a boundary consisting of middle wave and long wave light, the cell would have appeared to be directionally selective. Moreover, stimulation with long wave light alone, and then with long, middle and short wave light also resulted in a brisk discharge from the cell (see Fig. 9A). Such preliminary experiments showed that the cell was most sensitive, not to the presence of middle wave light, but to a change from long to middle wave light or to the addition of middle to long wave light. It was not surprising to find, therefore, that when the red, green and blue areas were placed in the receptive field and when each was made to reflect 69, 33 and 6 units of long, middle and short wave light, the cell did not respond to any of the areas, regardless of its colour (Fig. 9B), when the three projectors were switched on simultaneously. However, if while maintaining the above reflected energies from each area, the order in which the projectors were switched on was varied (thus leading to changes in the wavelength composition of the light reflected from the area in the cell's receptive field), the cell could be made to react (Fig. 9B). Thus, with the red area of the display in the cell's receptive field, if the long wave projector alone was switched on first and then, after a delay, the middle and short wave projectors added, the cell gave a response. Note that with all three projectors switched on, the red area was reflecting 69, 33 and 6 units of long, middle and short wave light, i.e. precisely what the same area was reflecting when all three projectors were turned on simultaneously and the cell did not respond. Similar responses were obtained from the white area, but when the identical experiment was done with the blue area the cell gave only a weak response and with the green area none at all.

The absence of a response to the green area, either when all three projectors were switched on simultaneously, or when the long and short wave lights were added to the long wave, might suggest that the cell was indeed responsive to colours. If so, it was to the "wrong" colour, for if one were to equate middle wave light with green, one would have expected it to respond to the green area! Moreover, using the same sequence of stimulation, the cell could be made to respond to the green area by simply changing the relative amounts of long and middle wave light reflected off the green area, without changing the colour as perceived by humans (Fig. 9C). Also, the responses of the cell to the red area, or to an area of any other colour, could be enhanced, reduced or abolished, by changing the relative amounts of long, middle and short wave lights reflected off the area in the cell's receptive field. This is shown in Fig. 9C.

In fact, there were some wavelength-selective cells whose responses were not as clear as the ones described above. For example, a long wave selective cell might give no response.
Fig. 9B. The responses of the cell Fig. 9A to the red, white, green and blue areas of a multicoloured display, when each was placed in its receptive field and made to reflect 69, 33 and 6 mW·Sr⁻¹·m⁻² of long, middle and short wave light (I). In II, the response of the cell is shown when, instead of illuminating the same areas with all three projectors simultaneously, the long wave projector was switched on first followed by the middle and short wave projector (the latter two were switched on simultaneously). Note that in II when all 3 projectors were switched on, each area reflected the identical triplet of energies as in I.

Fig. 9C. The responses of the cell of Fig. 9A to illumination of a green (upper two traces) and a red (lower two traces) area of a multicoloured display. Conventions as in previous Figures. The reflected energies were as follows: Upper left: LW = 19; MW = 135; SW = 17; Upper right: LW = 60; MW = 107; SW = 5; Lower left: LW = 20; MW = 20; SW = 6; Lower right: LW = 8; MW = 75; SW = 7.
as expected, when a green area of the display was put in its receptive field and illuminated with middle and short wave light alone. Adding long wave light might still not yield a response from the cell. When this happened, it was always possible to obtain a response from the cell by increasing the relevant wavelength. In the example given above, the long wave cell could be induced to respond to the green area if the amount of long wave light reflected was sufficiently increased, without changing the colour.

Every single wavelength-selective cell that was isolated in this study, whether it had frank opponent inputs or whether it responded to one part of the spectrum only, showed by its responses that it was sensitive to changes in the wavelength composition of the light reflected from an area, regardless of its colour. That is, a cell would respond, or not, to an area of any colour depending upon the sequence with which that area was illuminated, and hence the manner in which the wavelength composition of the light reflected from that area changed. Moreover, if a cell was unresponsive to one sequence of illumination it could be made to respond to it by changing the relative intensities of the light of the three wavelengths reflected off an area. Alternatively, if a cell was responsive to one sequence of illumination, its response could be reduced, or abolished, by the same means. In fact, one could derive an almost linear relationship between the amount of long, middle and short wave lights needed to activate or inhibit wavelength selective cells. Figure 10 shows this.

A red area of the multicoloured display was put in the receptive field of four cells whose action spectra showed them to be sensitive to long wave light only. As described above, each cell was excited by illuminating the display with long wave light and inhibited by adding middle and short wave light, in that order. The amount of middle and short wave light needed to inhibit the response to long wave light was tested in the following way. For each reading, the intensity of the long wave light was varied. When the long wave projector was switched on, and the cell responded to it, I determined, for each setting of long-wave light intensity, the amount of middle and short wave light needed to inhibit the response of the cell to long wave light. Predictably, the graphs show that as the amount of long wave light was increased so the amount of middle and short wave lights needed to inhibit the cells also increased.

In summary, then, the reaction of the WL cells described here depended critically on changes in the wavelength composition of the light reflected from the area in their receptive field, independently of the colour. The sequence with which the area in their receptive field was illuminated with lights of different wavebands was also critical in eliciting a reaction from them.

**DISCUSSION**

The experiments described in this paper and elsewhere* show that cells which, in the past, have been considered to be “colour-coded” are in fact sensitive to wavelengths and to changes in the wavelength composition of the light reflected from surfaces, and that their responses do not correlate with perceived colours. They thus reinforce the conclusion that there is, at the level of the single cell, a fundamental distinction between wavelength and colour.

It should, of course, be obvious that the responses of cells which are so sensitive to changes in the wavelength composition of the light reflected from surfaces cannot correlate with perceived colours, for colours remain largely stable in spite of continuous variations in incident and reflected wavelength composition. Imagine the difficulties that an animal would face if it had to depend solely on WL cells for recognizing differences between objects which we recognize by colour, e.g. the difference between a ripe and unripe orange. It would be in the odd situation of recognizing a ripe orange in one set of circumstances and not in another, perhaps seconds later, because of a change in the wavelength composition of the light reflected from it. But to maintain the stability of colours, the nervous system must be informed of changes in the wavelength composition and take account of them. This, presumably, is one function of the WL cells described here. It would, of course, be very interesting to learn how the information analyzed by these cells is used at subsequent stages of the visual pathways and how the detection of changes in wavelength composition contributes to the construction of colours by the cerebral cortex.

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REFERENCES


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