The Relationship Between Wavelength and Color Studied in Single Cells of Monkey Striate Cortex

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The study of color vision is technically no more difficult, or easy, than the study of other branches of sensory physiology. But it presents a formidable problem conceptually. Here, more than any other branch of sensory physiology, there is a schism between our perceptions and physical reality. Indeed, in terms of physical reality, color vision is perhaps the greatest of all sensory illusions. The most refined measuring instruments may tell us that the amounts of different wavelengths of light reflected off two surfaces, one red and the other green, are identical. Yet our nervous system reports them to be different in color (Land, 1977). This is fortunate, for the amount of light of different wavelengths reflected off any surface varies continuously during the day. If the color of objects and surfaces were to vary accordingly, then color vision would lose its significance as a biological signalling mechanism. If an orange, for example, were to appear red in one set of circumstances, green in another, and yellow in a third, then the presence of an orange would no longer be signalled by its color but by some other attribute. Because of the biological value of maintaining the constancy of colors, the nervous system has elaborated a set of rules which makes, within very wide limits, the amount of light of different wavelengths reflected off a surface irrelevant in determining its color. Indeed, to the nervous system, it is physical reality that is an illusion!

This illusory relationship between the physical reality and the perceptual reality is perhaps the root cause of much of the difficulty in studying color vision. Here I want to address myself to but one problem that has been the source of much confusion, namely the relationship between wavelength and perceived color as studied in single cells of the primate visual cortex.

It is now almost three centuries ago that Newton (1704) stated unambiguously that light itself is not colored. He wrote:

"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, and Violet-making and so of the rest. And if at any time I speak of Light as coloured or as endued with colours, I would be understood to speak not philosophically or 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." (my italics).

However, even though light itself has no color, it is common knowledge that the
visible spectrum appears colored to us, short-wave lights looking blue, middle-wave lights green and long-wave lights red. Between the physical reality of the colorless wavelengths of light and our perceptual reality of it as colored is a gulf so great that we suppose intuitively that light itself is colored and interpret our physiological results accordingly, without probing into the more fundamental question of why, if light itself is colorless, the visible spectrum looks colored to us (Land, 1981). Because middle wave light looks green, we suppose it to be green and because green objects have a higher reflectance for middle wave than for short and long wave light, we also suppose that the excess of middle wave light reflected off a surface makes it look green. Newton (1704) himself so believed. He 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" (my italics). In other words, to Newton, a red surface looks red because it reflects more long than middle or short wave light and a green surface green because it reflects more middle than short or long wave light. It is but one logical step from acceptance of this Newtonian equation of excess wavelength = color, to the further supposition that a cell in the nervous system that responds to middle-wave light only is a "green" cell responding best, or perhaps even only, to green surfaces, and a cell responsive to long-wave light only is a "red" cell. This is perhaps what all neurophysiologists have assumed, either implicitly or explicitly. A further supposition is that a cell giving an ON response to long-wave light and an OFF response to middle wave light is a "Red-ON, green-OFF" cell. Such cells have been thought to provide a neuro-physiological basis for Hering's Opponents Theory of Color Vision (see, for example, Boynton, 1979).

There is thus a chain of logical steps leading from our perception of the visible spectrum as colored to our supposition that the spectral selectivity of a cell is a guide to its color preference. It is worth examining the truth of the steps in this chain.

If Newton's supposition that the excess of wavelengths in the light reflected off a surface determines its color is true, then a green surface that reflects more long wave than middle or short wave light should look red, not green. In fact, as Land (1974, 1977) has shown in a series of rigorously controlled experiments, the color of a surface in a complex, multi-colored scene is independent, within very wide limits, of the wavelength composition of the light reflected off it. Thus, a green surface continues to look green even if it reflects more long wave than middle or short wave light and a white surface continues to look white even if it reflects the identical amount of long, middle and short wave light that a green surface reflects. Hence the second part of Newton's statement is not true for the perception of colors in a complex, multi-colored scene, i.e. in most natural situations. The predominance of light of any waveband reflected off a surface does not determine the color of that surface. One step in our logical chain is thus untrue. It necessitates a re-examination of the subsequent steps. This is that a cell that responds to, say, long wave light only is necessarily a "red" cell, responding best, or only, to red surfaces, and a cell that is responsive to middle wave light only is a "green" cell. Such cells have been found in monkey striate cortex, (Lennox- Buchthal, 1965; Dow, 1973; Gouras, 1974; Michael, 1978). They are commonly called opponent color cells and designated as R+ if responsive to long wave lights only, G+ if responsive to middle wave lights only and R+G+ if they give an on response to long wave lights and an off response to middle wave lights. Let us suppose that they are indeed "color coded" cells and test that supposition.
To do this, we isolated single, wavelength selective cells in monkey striate cortex (V1). The first step was to plot their receptive field and wavelength sensitivity curve (action spectra) in the traditional manner (see Zeki, 1977, 1978). Next the cells were studied using the same experimental paradigm as Land (1974, 1977) used in his perceptual experiments on color vision. The only difference is that whereas Land was studying the responses of human observers, we were studying the responses of single cells. Specifically, “Color Aid” papers of different color and of the size of the cells’ receptive field were placed in the receptive field against a black velvet cloth; alternatively different colored rectangles of a multicolored Mondrian display were placed in the receptive field in such a way that the rectangle coincided with the borders of the receptive field. In practice, for narrow band cells in V1, it makes little difference whether one uses a small colored patch in a multi-colored display, or a piece of colored paper in isolation. The description given below can thus be applied to either situation. The screen facing the animal, including the receptive field, could be illuminated with three 350 W projectors, each equipped with a band-pass filter, one passing long wave light only, another middle-wave light only and the third short-wave light only (see Land and McCann, 1971). A rheostat attached to each projector allowed variations in the intensity of light coming from each. The amount of light reflected off the area in the cell’s receptive field when each projector was turned on alone could be read by means of a Gamma Scientific telephotometer, equipped with an equal energy filter. In the description given below, whenever I refer to color, I mean color as perceived by human observers since there is no device, besides the human visual system, that can measure color. With such an experimental paradigm we are in a position to test rigorously the proposition that excess wavelengths = perceived color and that therefore wavelength selective cells are necessarily “color coded”. Here, the description is restricted to wavelength selective cells in monkey striate cortex.

Proposition I: Light of long wavelengths appears red to human observers and light of middle wavelengths appears green. We suppose therefore that a wavelength selective cell in monkey striate cortex that responds to long wave light only will respond to red surfaces and one that responds to middle wave light only will respond to green surfaces. Since a surface will continue to appear red (or green) to human observers even in spite of wide ranging variations in the amounts of long, middle and short wave-bands in the light reflected off that surface, we suppose further that a cell selective for long wavelengths will respond to a red surface as long as it appears red to human observers, i.e. regardless of the wavelength composition of the light reflected off it.

Fig. 1 shows the responses of a cell in monkey striate cortex. Its wavelength sensitivity curve (action spectrum) was plotted by shining monochromatic light of different wavelengths onto the receptive field, and noting the minimum intensity at every wavelength which elicits a response from the cell. The action spectrum so plotted showed that the cell was responsive to long wave light only. (That it did not respond to light of other wavelengths or to white light suggests that it must have received an opponent input from light of other wavelengths, perhaps at some antecedent stage of the visual pathways.) Because long wave light looks red to us, one might suppose that it will respond to a red surface only. To test this, a red area of a multicolored Mondrian display was put in the receptive field of the cell and the
Fig. 1. The response (shown as the discharge frequency) of a wavelength selective cell in V1 to different colored areas of the Mondrian display (right). In column A, each area when placed in the cell’s receptive field, was made to reflect 69, 33 and 6 mW·Sr⁻¹·m⁻² of long, middle and short wave light. In column B, the amount of long wave light was increased, without entailing a change in perceived color, until the cell responded. The action spectrum of the cell is shown to the left, a parabola being drawn through the experimentally determined points. The reaction of this cell, as well as those of Figs. 2 and 3, were studied with monocular stimulation.

display illuminated with all three projectors. By varying the intensities of the three projectors, the red area was made to reflect 69, 33 and 6 mW·Sr⁻¹·m⁻² of long, middle and short wave light. The area appeared a vivid red to human observers. When the shutters were opened, the cell did not respond (trace IA). Next, the amount of long wave light coming off the red area was increased, but the area still looked a vivid red to human observers. Now the cell gave a response to the same red surface (trace IB). Similar responses were obtained from other cells whose wavelength sensitivity was restricted to long wavelengths. When the reaction of cells sensitive to middle wave light only, to green areas placed in their receptive field, was studied, identical responses were obtained. In other words, the cells responded or not to the green area depending upon the amount of middle wave light reflected off it even though the area always looked green to human observers.

Proposition I is therefore false. A long wavelength selective cell in monkey striate cortex does not respond to a red area per se. It may respond to it or not depending upon the amount of long wave light reflected off its surface, and regardless of its color, just as a middle-wavelength selective cell may or may not respond to a green
area placed in its receptive field depending upon the amount of middle wave light reflected off its surface. Thus the responses of these wavelength-selective cells cannot be correlated with the perceived color.

**Proposition II:** Even though a cell which is responsive to long wave light only may or may not respond to a red area, depending upon the amount of long wave light reflected off it, it is still selective to color in that it will not respond to an area which appears, say, white or yellow or blue to human observers, no matter how intense the amount of long wave light reflected off these areas.

Fig. 1 shows the responses of the wavelength selective cell, responsive to long wave light only, to the white, green and blue areas of a Mondrian display. Each area, when placed in the cell’s receptive field, was made to reflect 69, 33 and 0 mW·Sr⁻¹·m⁻² of long, middle and short wave light although each area retained its color. The cell did not respond to any of the areas, including the red one. However, it could be made to respond to each area if the amount of long wave light was sufficiently increased, even though with such increases the color of the area in the cell’s receptive field did not change.

All the wavelength selective cells in V1 that were tested (34) behaved in a similar way, i.e. regardless of their action spectrum, they either did not respond, or responded, to an area of any color placed in their receptive field when the amount of long, middle and short wave light reflected off the areas was identical. If the cell did not respond, it could be induced to do so by increasing the amount of light of its preferred wavelength reflected off the area in its receptive field, without changing its perceived color. If it did respond, its response could be reduced or abolished by decreasing the amount of its preferred wavelength in the reflected light, without changing the color. The cells were thus unable to distinguish between the colors. Proposition II is therefore false.

**Proposition III:** A cell that gives an ON response to middle wave light and an OFF response to long wave light (or vice versa) is a red ON-green OFF cell (or vice versa), being excited by a red surface and inhibited by a green one. Its responses can be correlated with the perception, by humans, of red and its after image and it is this activity in many cells which is the basis of the psychophysically observed colored after images.

Fig. 2 shows the responses of a long wave light OFF, middle wave light ON cell (see inset for its action spectrum). When a red area of the Mondrian display was placed in the receptive field and made to reflect more long than middle wave light, the cell did not give a response when the shutters were opened, but responded when they were closed, i.e. it gave an OFF response (trace B). But when the red area was made to reflect more middle wave than long wave light, and still looked red to human observers, the cell responded at ON but not at OFF (trace A). I emphasize that for human observers the after image produced by viewing the red area in either of the two conditions mentioned above was green. Hence the responses of the cell could not be correlated either with the perceived color or the color of the after-image produced by viewing that area. Next the green area of the Mondrian display was placed in the receptive field of the cell and arranged to reflect more middle than long wave light. The area looked green to human observers and its after image was red. The cell responded at ON but not at OFF (trace C). When the same green area was
made to reflect more long than middle wave light, and the area still looked green to human observers, the cell responded at OFF but not at ON (trace D). In the latter instance, the after image produced by viewing the green area was still red. Other cells with frank opponent inputs behaved in the same manner. Thus the responses of the cells could not be correlated with color but only with the “excess and predominance” of light of the relevant wavelength. Proposition III is therefore false.

These experiments show:

(a) that the perceived color of a surface does not depend upon the wavelength composition of the light reflected off that surface (Land 1974, 1977). The reaction of the wavelength selective cells in V1, by contrast, does depend upon that composition, the cells responding, or not, to a surface of any color depending upon the amount of light of their preferred wavelength that is present in the light reflected off a surface, and independently of its color;

(b) that the Newtonian equation of excess wavelength = perceived color is not, in general, true perceptually but that the notation excess of relevant wavelength = response from a wavelength selective cell of V1 is true, (but see below);

(c) that it follows from (a) and (b) that the wavelength selective cells of V1 are not “color-coded”;
(d) that since the perceived color of a surface is independent of the wavelength composition of the light reflected off it, so is the after image. In other words, that the after image also does not obey the rule excess wavelength = perceived color = color of after image;

(e) that it follows from (d) that the responses of these opponent input cells of V1 cannot be the direct basis of the colored after-image; and

(f) that the action spectrum of a cell is not necessarily a guide to which colors it will respond to.

There are, of course, cells in the visual cortex of the rhesus monkey whose responses do correlate with the perceived color. The responses of these cells, by definition, are independent of the wavelength composition of the light reflected off a surface, and correlate with the color alone. Such cells have been found in V4 (Zeki, 1980) and need not be further described here. They too have narrow action spectra. If one were to restrict one’s study of wavelength selective cells to a study of their action spectra, one might well reach the conclusion that there is no difference between cells in V1 and in V4. More sophisticated studies, reported here, reveal a radical difference.

I have alluded above to the fact that perceptually, the Newtonian notation of excess wavelength = color is not, in general, true. There is however, one situation in which it is true, one which we may call the Newtonian context. If one were to look at a small patch in a void, so that one can only see that small patch and nothing else, and illuminate that patch with three projectors, the perceived color of that patch, no matter what its color is in normal surroundings, will depend upon the wavelength composition of the light reflected off it. Thus, if a red patch is viewed in this Newtonian void, and intensities so arranged that the patch reflects more middle than short or long wave light, the patch will appear perceptually green. If a patch of paper which appears green in normal surroundings is viewed in a Newtonian void and the intensities from the projectors so arranged that the green patch is made to reflect twice the amount of long wave than of middle or short wave light, it will appear perceptually gray. Since in this Newtonian situation our perception of colors is determined by the excess of wavelengths in the reflected light, it seemed interesting to ask whether the response of the wavelength selective cells in V1 is also always determined by the presence of an excess of light of their preferred wavelength in the light reflected off a surface in their receptive field.

This would appear to be so for the cell of Fig. 1, since for that cell to respond the amount of long wave light reflected off the surface in its receptive field had to be far in excess of middle and short wave light. But this was not so for the cell of Fig. 3. This wavelength selective cell was responsive to middle wave light only. However, when a green or red patch was put in its receptive field and arranged to reflect 69, 33 and 6 mW · m⁻² · m⁻² of long, middle and short wave light, the cell responded to either area with almost equal vigor and without distinction. When these two areas, reflecting the above amounts of light, were viewed in isolation, they looked pinkish gray, not green. Hence, although the equation, excess wavelength = perceived color in the Newtonian void is true, this is not necessarily so for the wavelength cell of V1 described above since it responded when the amount of middle wave light, to which it was selective, was less than the amount of long wave light. We thus modify (b) above and write:

“Sufficient amount of light of relevant wavelength = response from a wavelength selective cell in V1”.
Fig. 3. The responses of a middle-wavelength selective cell in V1 (see inset for its action spectrum) to the red and green areas of a Mondrian display. Each area, when placed in the cell’s receptive field, was made to reflect 69, 33 and 6 mW·Sr⁻¹·m⁻² of long, middle and short wave light.

The term sufficient can be defined operationally, in terms of a cell’s response, since some middle wave selective cells give a response if the amount of middle wave light is less than the amount of long wave light (as in Fig. 3) whereas for others the amount of middle wave light has to be in excess.

The interest in viewing patches of color in isolation arises from the fact that there may be similarities between this perceptual situation and the responses of cells in V1. When we view a patch in isolation our perception of its color depends upon the wavelength composition of the light reflected off it alone, and is unaffected by anything in the surround. The striate cortex of the monkey receives a “point-to-point” projection from the retina. Anatomical work (Fisken et al., 1973) shows that the lateral connections of each small region of the striate cortex are limited to 1–2 mm. In other words, the cells in each part of the striate cortex “look” at a small part of the field of view and are not influenced by what goes on elsewhere, at least not by the activity of cells lying beyond 1–2 mm (Hubel and Wiesel, 1977). Since our perception of colors as constant depends upon comparing reflectances from extensive parts of the field of view, it follows that the wavelength selective cells in V1 which are unable, because of their restricted connections, to make such comparisons, can react to the wavelength composition alone, and not to color. This is, of course, speculative and it is possible that the double-opponent cells that Michael (1978) has found in monkey striate cortex do respond to colors as such. It is, however, striking that the lateral connections in V4, where color-coded cells have been found (Zeki, 1980), are much more widespread than those in V1 (Zeki, unpublished results).

My aim in this work was to show that the wavelength sensitivity curves of the wavelength selective cells cannot predict whether a cell is color coded or not. It
follows that to give an adequate description of the neurophysiology of color vision, a much more detailed study is required, one in which the reaction of cells to colors in natural situations is taken into account.

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REFERENCES