

Post-receptoral processes in colour vision

from J.D. Mollon

ALTHOUGH our subjective experience of hue may seem endlessly varied, the process of colour vision begins with just three classes of retinal receptor, each sensitive to a large part of the visible spectrum. Long before these delicate structures could be directly measured by physiologists, the limitation to three parallel channels was deduced by psychophysicists — those who work out the logic of sensory systems from the responses of conscious observers to systematically varied inputs. More difficult for the psychophysicist was the task of discovering how absorption varied with wavelength for the individual classes of receptor, since these 'spectral sensitivities' overlap substantially and it is not possible to isolate, say, the short-wavelength receptors simply by stimulating the retina with violet light. However, experimental stratagems were developed to cause an observer's response to depend on signals from only one class of receptor: for example, the psychophysicist might use monochromatic adapting stimuli to suppress two of the three classes or he might choose spatial and temporal parameters for his target stimulus that were suspected to favour one class of receptor or he might seek observers genetically lacking either one or two of the three classes. For many decades, psychophysical estimates of the receptor sensitivities differed widely, but the past 20 years have seen a quiet convergence on the wavelengths 440 nm (violet), 535 nm (green) and 565 nm (yellow green) for the peak sensitivities of the three classes; and although these values need correction for selective absorption in the media of the eye and although second-order disagreements remain, the psychophysical estimates are in first-order agreement with very recent physical measurements of individual receptors (see papers by Bowmaker and collaborators in *J. Physiol. Lond.*, 298, 1980).

Isolating opponent channels

It is generally held that a second kind of parallelism follows the receptor stage. There are some channels (loosely called 'luminance' or 'non-opponent' channels and probably needing further subdivision) that receive signals of the same sign from the receptors with peak sensitivities at 535 and 565 nm, and there are others (the 'colour-opponent' channels) that receive antagonistic signals from different classes of receptor. The colour-opponent channels extract information about wavelength by comparing the relative absorption in different classes of receptor. (The receptors themselves, of course, are individually colour-blind, since they are broadly tuned and since a photon, once

absorbed, yields the same signal whatever the wavelength of the stimulating light.)

Psychophysicists have developed stratagems to isolate individual channels at this second stage and several experimental techniques for isolating opponent channels became explicit at a meeting on post-receptoral processes held in London on 9 January by The Colour Group, an interdisciplinary society linking those with physical, physiological, and aesthetic approaches to colour.

If detection thresholds are measured for weak monochromatic stimuli presented on various steady adapting fields, detection by opponent channels is favoured if the targets are of long duration or large area — presumably because these channels integrate in time and space more than do (some) non-opponent channels. Evidence for this position was presented at the meeting by E. King-Smith (University of Manchester) and by D.H. Foster (University of Keele).

King-Smith suggested that strong, white-adapting fields will adapt non-opponent more than opponent channels, because the sensitivity of the latter is controlled by the difference in signals from different receptors and so will change little with absolute light intensity. J. Mollon (Cambridge University) added the complementary suggestion that strongly coloured, monochromatic fields (as used classically by Stiles) cause detection to depend largely on non-opponent channels, because such fields disproportionately desensitize opponent channels.

Foster described a new technique for isolating opponent channels. On a standard adapting field is superimposed a small, steady 'auxiliary' field, which is congruent with the target flash. If, say, the target is of long wavelength and only the main adapting field is present, the field is most effective in reducing sensitivity when its wavelength is ~570 nm; introduction of the auxiliary field shifts the wavelength of maximal field sensitivity to ~610 nm, suggesting that detection now depends on a channel which receives excitatory signals from the 565-nm receptors and antagonistic signals from the 535-nm receptors. The effect of the auxiliary field is abolished if the auxiliary field is significantly larger than the target spot. Presumably the presence of a contour coincident with that of the target masks a spatial transient that would otherwise allow detection by a non-opponent channel.

Mollon proposed that detection will depend only on an opponent channel if the input signal is confined to the violet-sensitive receptors. Perhaps because the short-wavelength component of the retinal image is usually out of focus (owing to the chromatic aberration of the eye), signals from the violet-sensitive receptors seem to

be used only to provide information about hue. Because these receptors are far removed in peak sensitivity from the other two classes, the sensitivity of the opponent channel can be modulated with long-wavelength fields without significantly changing the rate of photon absorptions in the violet-sensitive receptors themselves — a great experimental convenience.

According to a hypothesis of Pugh and Mollon (*Vision Res* 19,293; 1979), an opponent channel is most sensitive to input perturbations when it is near the middle of its operating range. In collaboration with P.G. Polden and A. Stockman, Mollon has found large oscillations in sensitivity to violet targets during adaptation to a bright yellow field; these are thought to arise from changes in the balance of inputs to the opponent channel during bleaching of the long-wavelength receptors. King-Smith reported that in several ocular diseases (for example, retrobulbar neuritis and glaucoma) patients show a greater loss of sensitivity to short-wavelength targets when the eye is adapted to a yellow field than when the adapting field is white and relating this finding to the above hypothesis proposes that the operating range of opponent channels is reduced in disease.

It is well established that adaptation to a visually presented grating will briefly raise the threshold for a subsequently presented 'test' grating of similar orientation and spatial frequency. K. Ruddock (Imperial College, London) has previously reported that if the adapting and test gratings are presented to one eye, a low-frequency spatial pattern presented to the other eye during adaptation will reduce the extent of adaptation. V. Waterfield and he have now shown that the effectiveness of this contralateral stimulus depends on its wavelength. Moreover, variation of its actual pattern intriguingly reveals channels of different spectral sensitivities: thus a simple grating gives the photopic luminosity function, a pattern of blobs reveals a long-wavelength channel with opponent inputs from the 565-nm and 535-nm receptors, and the negative of the latter pattern gives a green-sensitive mechanism with a small inhibitory long-wavelength input.

Two possible pitfalls

Many papers in the recent literature have advanced a further stratagem for isolating colour-opponent channels: the observer is required to detect a spatial or temporal transition between stimuli that are of different wavelength but equal luminance. However, I feel that it is unlikely that this device will safely eliminate detection by 'luminance' channels. Suppose that the target is a red field briefly substituted for a white field of equal luminance. At the onset of the red field, an increment is presented to the 565-nm receptors and a decrement to the 535-nm receptors. We are

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obliged to adopt an assumption for which there is no proof, that the transient responses generated in the two classes of receptor will exactly cancel out in all the putative 'luminance' channels; we must suppose that the weightings of inputs from the different receptors are in a constant ratio for all channels and that the transient waveforms of different signs are symmetrical. Transients in space and time are biologically significant and it would be odd if the retina allowed them to be lost in this way.

A second pitfall may lie in relating the detection measurements mentioned above directly to the classical phenomenological measurements (see for example Hurvich & Jameson *Psychol. Rev.* 64, 384; 1957) that kept alive the concept of opponent processes during a period of neglect. General understanding of the first stage of colour vision was earlier held back by a widespread but unjustified belief that the peak sensitivities of the three receptors should correspond to phenomenologically primary colours, red, green and blue; it may equally be a mistake to suppose now that the opponent processes of the retina must be directly related to the phenomenological oppositions of blue and yellow and of red and green. S. Zeki (University College, London) presented his measurements of the spectral sensitivities of individual nerve cells in Area V4 of the cerebral cortex of the rhesus monkey; even at this central level, although many cells have narrow bandwidths (10–20 nm), the peak sensitivities do not cluster very tightly at the four phenomenologically pure hues, blue, yellow, green and red, but are distributed throughout the spectrum, with possibly a gap at 560–570 nm.

Colour constancy

As we view an object from different distances and angles or under different illuminations, our perception changes much less than does our retinal image. This stability of our perception is known as perceptual constancy. It is an everyday observation that a sheet of white paper looks equally white in daylight and in the yellowish illumination of domestic tungsten light, although if outdoor film were used to photograph the paper indoors, the resulting transparency would have a strong yellow cast. The correction achieved by our visual system (but not by the photographic process) is called colour constancy. One of the most interesting results presented at the meeting was Zeki's finding that some individual cortical cells show colour constancy: if an array consisting of many different coloured patches is placed before a monkey, and, say, a green patch is arranged to cover the receptive field of a green-sensitive cell, the cell responds to the patch despite gross changes in the spectral composition of the illumination falling on the array; but the cell does not respond if, say, a red patch is placed in its receptive field and the overall illumination

is adjusted so that the spectral composition of the flux reflected from the red patch was identical to the flux previously reflected from a green patch to which it did respond (Zeki *Nature* in the press). Under the latter condition, of course, the patch looks red, not green, to a human observer (see *Land Sci. Amer.* 237, December; 1977) just as, in the classical demonstration of size constancy scaling, an after-image of fixed retinal dimensions looks of different sizes when projected on surfaces at different distances.

Colour preferences

The layman reasonably expects the colour scientist to be much concerned with people's colour preferences, but the experimental study of colour preference has an unhappy history of inconsistent results and has been neglected in recent years. Reviewing this field for the meeting, I.C. McManus (Bedford College and St. Mary's Hospital, London) noted that earlier

studies had confounded variation in hue with variations in saturation and lightness, and he described a study, performed in Cambridge in collaboration with A. Jones and J. Cottrell, in which this failure was corrected. Another feature of this new study was the use of the 'method of paired comparisons': each of a large set of coloured chips was paired with every other chip and the subject was asked to express a preference between the members of each possible pair, thus allowing the experimenter to derive a measure of internal consistency. When saturation and lightness are held constant, the population shows a clear preference for blue and a clear dislike of yellow. Further analysis shows differences between individuals but consistency within an individual's data; differences between individuals seem to be almost entirely due to differences in lightness preference and saturation preference, with very small inter-subject differences in hue preference. □



100 years ago

THE CRAYFISH¹

Common and lowly as most may think the crayfish, it is yet so full of wonders that the greatest naturalist may be puzzled to give a clear account of it." These words from von Rosenhof, who in 1755 contributed his share to our knowledge of the animal in question, are cited by Prof. Huxley in the preface to the careful account of the English crayfish

¹"The Crayfish: an Introduction to the Study of Zoology." By T.H. Huxley, F.R.S. (London: Kegan Paul, 1880.)

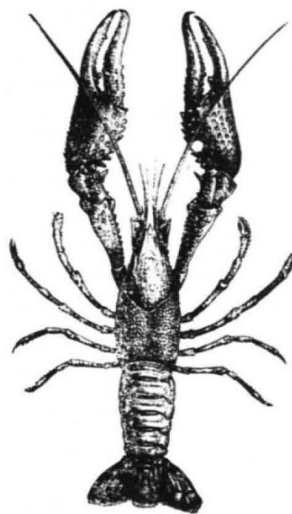


FIG. 4.

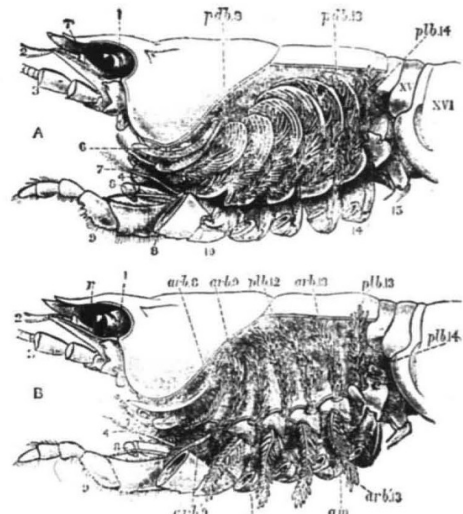


FIG. 5.

From *Nature* 21, 12 Feb., 353; 1880.