

## Perception

# Questions of sex and colour

from John D. Mollon

"WHEN I look at that purple clematis, do I have the same colour sensation as you?" When this familiar question is put to him, the professional colour scientist will deftly refer the questioner to Wittgenstein. But there is a more tractable question that he will discuss for hours: if we take any two healthy people (excluding those who are explicitly colour blind) and if we find two different spectral mixtures that look the same to observer A, then will the mixtures always match for B?

On page 623 of this issue<sup>1</sup>, Jay Neitz and Gerald Jacobs report that there are two distinct types of men within the population that we call 'colour normal', and that there are three types of women. The authors postulate a polymorphism at the locus on the X chromosome that specifies the long-wave (red-sensitive) photopigment of the retina. Because men are XY, they can inherit only one or other of the two alleles envisaged by Neitz and Jacobs. There should be homozygous women who resemble each of the male hemizygous types; but a third class of women will be heterozygous at the locus and should exhibit an intermediate form of colour vision.

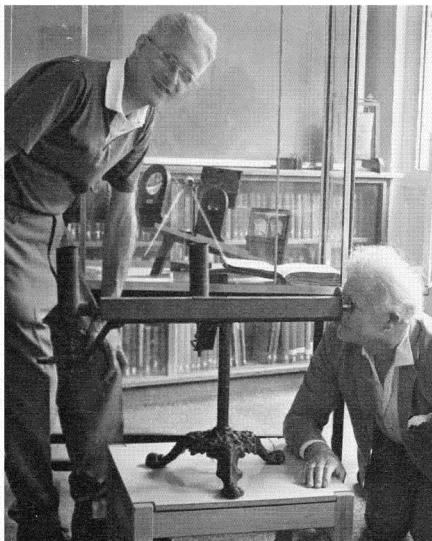
The perceptual test used by Neitz and Jacobs is a variant of one described in *Nature* in 1881 by Lord Rayleigh<sup>2</sup>: the observer is shown a patch of monochromatic orange light (the sodium line at 589 nm in Rayleigh's experiments) and is invited to match it by adjusting the ratio of red to green illuminating a second patch. Provided he is allowed to adjust, if necessary, the radiance of the orange field, the colour-normal observer is able to make the two fields look identical. He can do this because the short-wave cones of the retina are very insensitive in this part of spectrum and the observer needs only to adjust the red/green ratio to give a ratio of quantum catches in his long- and middle-wave cone receptors that is the same as the ratio produced by the orange light<sup>3</sup>.

Neitz and Jacobs' test differs in at least three ways from the classical 'Rayleigh match': (1) the stimulus field is large, with an outer diameter of 11 degrees and an occluded foveal region; (2) the fields to be matched are not adjacent but are substituted for each other in time; and (3) the monochromatic field has a wavelength of 600 nm and the red primary is at the very long wavelength of 690 nm.

In the history of colour science, bimodalities among colour-normal observers have often been suggested, and often denied. There have been recurrent reports of a bimodality in the wavelength

judged to be 'unique' green, the green that is neither bluish nor yellowish<sup>4,5</sup>; but this bimodality has proved difficult to replicate<sup>6,7</sup> and the physiological basis for the judgement is uncertain.

More relevant to the new results is the



The 'anomalouscope' used by Lord Rayleigh in 1881 to study individual differences in colour matches. This photograph was taken in 1973 while Rayleigh's instrument was being examined by two distinguished scientists, M. Alpern (left) and the late W.A.H. Rushton.

work of Georg Waaler<sup>8,9</sup>, a retired Norwegian forensic scientist who also measured Rayleigh matches. Using the Nagel anomalouscope (Model II), a clinical instrument, Waaler obtained a series of matches for different wavelengths of the monochromatic field between 574 and 603 nm. He claimed that his male observers fell into two clear groups,  $G_1$  and  $G_2$ , according to whether they used more or less red in their matches; occasional matches might be out of line, but the set of equations for an individual allowed a clear diagnosis. Postulating the same mode of inheritance as do Jacobs and Neitz, Waaler showed that  $G_1$  sons never have  $G_2$  mothers and  $G_2$  sons never have  $G_1$  mothers. The new results of Jacobs and Neitz should cause us to look afresh at Waaler's long-neglected claims.

Neitz and Jacobs reported their remarkable results at a meeting of the Optical Society of America last year. At about the same time, visual scientists began to learn of the work of Jeremy Nathans and his collaborators on the molecular genetics of colour vision (refs 10, 11; see my previous *Nature and Views* article<sup>12</sup>). Nathans' group showed that the X chromosome often carries more than one copy of the gene for

the middle-wave pigment, but there is never more than one copy of the gene for the long-wave pigment. Neitz and Jacobs, on the other hand, postulated variation in the long-wave gene. Many saw here a clear inconsistency.

In fact, there is no contradiction in the results so far published. Nathans and his colleagues sequenced only the two middle-wave genes of Nathans' own X chromosome. The two sequences differ only in a 'silent' substitution of one nucleotide, a substitution that would leave unchanged the sequence of amino acids in the photopigment molecule specified by the gene. In principle at least, it is possible that the middle-wave gene varies in number and the long-wave gene varies in sequence. The conclusion of Neitz and Jacobs depends critically on assumptions about the relative sensitivities of the middle- and long-wave pigments near 690 nm; but it is not actually contradicted by the published molecular genetics, and there is direct microspectrophotometric evidence for individual differences in the human long-wave pigment<sup>13</sup>.

The bimodality reported by Neitz and Jacobs is impressive and it is difficult to imagine an experimental artefact that could generate a bimodality. But the psychophysical cognoscenti will enjoy trying to think of alternative physiological mechanisms. It might be argued that some observers do, whereas others do not, attend to a signal from a third receptor system, for the spectrum locus between Neitz and Jacobs' two primaries (546 and 690 nm) is not strictly dichromatic<sup>14</sup>. Or one might suppose that sensitivity to the 690 nm primary varies with individual differences in body temperature. In the far red, the probability of absorption of a quantum depends both on its intrinsic energy and on the thermal vibrational energy possessed by the chromophore

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group of the pigment molecule<sup>15,16</sup>. By manipulating his own body temperature by only one degree, the physicist De Vries was able to demonstrate changes in his visual sensitivity to the far red<sup>17</sup>. Temperature variations of this order occur diurnally; in women there is a monthly variation. If Neitz and Jacobs' young men did cluster at two temperatures, it would be easy to explain why the bimodality was obscured in their young women.

But suppose there is a polymorphism of the long-wave pigment. Has it been main-

tained by a heterozygous advantage? In the squirrel monkey, a basically dichromatic species, there is almost certainly a polymorphism at the single locus that specifies a pigment in the red-green spectral region<sup>18,19</sup>. Heterozygous females become behaviourally trichromatic<sup>20</sup> because X-chromosome inactivation<sup>21</sup> segregates into different cones the products of the alternative alleles; the monkey's visual system seems plastic enough to exploit this added differentiation of cone cells. It has been suggested that the polymorphism is

in fact maintained by the advantage to the heterozygous females<sup>18</sup>. Our own species is basically trichromatic. So if many women are heterozygous for one of the photopigments, are they in fact tetrachromatic, enjoying an extra dimension of colour discrimination? And if they are, does it give them an advantage? □

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