Perception (2009) **38**, 832-834

Unlocked edges or contradictory edges?

Is there a master signal for edge locking?

In 1977, when Richard Gregory published his classic paper on equiluminance, it was conventional to model the visual system with two chromatic channels and one 'luminance' channel. The signals of the long- (L) and middle-wave (M) cones were summed in the putative luminance channel; and so this channel would be silent at an edge between surfaces of different colour but equal luminance. There was then no edge signal to corral the more diffuse signals carried by the chromatic channels. Gregory suggested that this loss of edge-locking led to the several curious features of vision at equiluminance.

The passage of 30 years has revealed a much larger number of parallel channels within the visual system. At least fifteen morphologically and functionally distinct types of ganglion cell are now known (Dacey et al 2003; Petrusca et al 2007), each extracting different combinations of cone signals. Each type tessellates almost the whole retina and has its own specific projections within the brain. These different cells vary vastly in the extent of their dendrites and thus, presumably, in the sizes of their receptive field.

On the one hand, this means that Gregory's question becomes a more general one: Is there one channel, carrying a spatially precise signal, that coordinates the signals representing other stimulus attributes, such as colour, flicker, and texture? On the other hand, it has become unlikely that all the types of chromatically non-opponent ganglion cell will look on in silence when an equiluminant red/green edge is swept across the receptor array (Mollon 1980). First, the non-chromatic cells may vary in their equiluminous points. Second, their responses may not be linear: transients signalled by different classes of cone may be transmitted without complete cancellation (see eg Cavanagh 1991; Mollon 1982). Certainly, the parasol cells—traditionally taken as the substrate for the luminance channel—give a frequency-doubled response to a red–green grating traversing their receptive field, and there is no relative intensity of the component colours at which the cell is silenced (Lee et al 1989). Only one special subset of equiluminous edges is invisible to parasol cells: these are tritan edges, those between chromaticities that give identical quantum catches in the L and M cones and differ only in the short-wave cone signal (Tansley and Boynton 1976).

The midget ganglion cells might be thought to be good candidates for carrying Gregory's master signal, since they have the smallest receptive fields. In the fovea, the midget cells—certainly the OFF type—draw their centre input from a single cone (Kolb and Marshak 2003) and so should offer the most precise local sign. Then, however, the issue becomes less straightforward. For the midget cells carry one of the main chromatic signals: at low spatial frequencies, they signal the ratio of L and M cone excitation. At high spatial frequencies, however, they respond to achromatic contrast, to local variations in luminance (Ingling and Martinez 1983; Lennie and D'Zmura 1988).

Central mechanisms might recover separately the chromatic information and the edge information—by comparing the outputs of the four subtypes of midget cell (L- versus M-centre, ON- versus OFF-centre) and by applying low-pass and band-pass spatial filters to the array of midget cell signals. Edge-locking of colour signals would then become an intrinsic part of this analysis, and it is less clear how the colour and the edge would become dissociated.

The instability of perception at equiluminance

In his 1977 paper, Gregory described the 'jazzy' and unstable appearance of a line of one colour on an equiluminous background of a different colour (see also Liebmann 1927/1996). He attributed this phenomenal lability to the loss of the edge-locking signal.

However, I have put forward an alternative view of why perception is unstable at equiluminance (Mollon 1987, 1989). Consider an edge between red and green areas. We cannot render the edge concurrently invisible to the L and M cones. The very difference between L and M spectral sensitivities makes it impossible to silence both at once. Let us use the convenient term of 'isolept', introduced by Rushton et al (1973) for the condition where different colours give equal quantum catches in one class of cone. Between the L and the M cone isolepts lies a special zone where contours are of opposite sign for the two classes of cone: one class sees an edge that passes from darker to lighter, whereas the second sees the opposite. Outside this zone, defined by the two isolepts, a red–green edge has the same sign for both classes of cone. Now, the point of equiluminance lies in this inter-isolept zone. It may be the contradictory signals of L and M cones that cause the 'jazzy' appearance of equiluminous stimuli.

The impairment of stereopsis and motion perception at equiluminance

Depth perception is abolished or impaired if the black and white elements of a random-dot stereogram are replaced by red and green elements equated in luminance (Gregory 1977; Lu and Fender 1972). Can this result be explained by the absence of an edge-locking signal? Does stereopsis fail because the exact position of a given colour is not available to the disparity-analysing system? An experiment by Kim and Mollon (2002) rules out this hypothesis.

In order to side-step the traditional problems of edge artifacts (whether introduced by the display or by chromatic aberration within the eye), Kim and Mollon superimposed a black grid on their red/green random-dot stereograms. Thus, individual red and green squares were not abutting but were always separated by a firm contour of high contrast. The latter served to mask any slight edge artifacts, but—for the purposes of the present argument—note that the superposed grid potentially provides a strong edge-locking signal for each coloured cell. To estimate the point of equiluminance we used a forced-choice performance task rather than phenomenal report: on each trial the subject indicated whether a target region lay in front of or behind the rest of the array, and the computer adjusted the radiance of the red elements to establish the value at which performance was poorest. There was always a setting at which stereopsis completely collapsed and performance was at chance. This also held for detection of motion in random-dot kinematograms.

Thus, stereopsis and motion perception can fail even when explicit edge signals are supplied. So an alternative, and rather traditional, hypothesis recommends itself: the mechanisms that extract depth or motion from random-dot arrays are colour blind, in the sense that they cannot use chromaticity to identify corresponding elements.

John D Mollon
Department of Experimental Psychology, University of Cambridge, Downing Street, Cambridge CB2 3EB, UK; e-mail: jml23@cam.ac.uk

References

Cavanagh P, 1991 "Vision at equiluminance", in *Vision and Visual Dysfunction* Ed. J R Cronly-Dillon, volume 5 *Limits of Vision* Eds J J Kulikowski, V Walsh, I J Murray (London: Macmillan) pp 234–250

Dacey D M, Peterson B B, Robinson F R, Gamlin P D, 2003 "Fireworks in the primate retina: in vitro photodynamics links dendritic morphology, physiology and connectivity of diverse cell types in the retinogeniculate pathway" *Neuron* **37** 15–27

Gregory R L 1977 "Vision with isoluminant colour contrast: 1. A projection technique and observations" *Perception* **6** 113–119

Ingling C R, Martinez E, 1983 "The spatiochromatic signal of the r–g channel", in *Colour Vision: Physiology and Psychophysics* Eds J D Mollon, L T Sharpe (London: Academic Press)

Kim Y-G, Mollon J D, 2002 "Conditions under which stereopsis and motion perception are blind" *Perception* **31** 65–71

Kolb H, Marshak D, 2003 "The midget pathways of the primate retina" *Documenta Ophthalmologica* **106** 67–81

Lee B B, Martin P R, Valberg A, 1989 "Nonlinear summation of M- and L-cone inputs to phasic retinal ganglion cells of the macaque" *Journal of Neuroscience* **9** 1433–1442

Lennie P, D'Zmura M, 1988 "Mechanisms of color vision" *CRC Critical Reviews in Neurobiology* **3** 333–400

Liebmann S, 1927/1996 "Über das Verhalten farbiger Formen bei Helligkeitsgleichheit von Figur und Grund", Dissertation Thesis, Friedrich-Wilhelms-Universität, Berlin; 1927 *Psychologische Forschung* **9** 300–353 [translated into English in West et al (1996)]

Lu C, Fender D H, 1972 "The interaction of color and luminance in stereoscopic vision" *Investigative Ophthalmology* **11** 482–490

Mollon J D, 1980 "Post-receptoral processes in colour vision" *Nature* **283** 623–624

Mollon J D, 1982 "Color vision" *Annual Review of Psychology* **33** 41–85

Mollon J D, 1987 "On the nature of models of colour vision" *Die Farbe* **34** 29–46

Mollon J D, 1989 "Tho' she kneel'd in that Place where they grew ..." *Journal of Experimental Biology* **146** 21–38

Petrusca D, Grivich M I, Sher A, Field G D, Gauthier J L, Greschner M, Shiens J, Chichilinsky E J, Litke A M, 2007 "Identification and characterization of a Y-like primate retinal ganglion cell type" *Journal of Neuroscience* **27** 11019–11027

Rushton W A H, Spitzer Powell D, White K D, 1973 "Exchange thresholds in dichromats" *Vision Research* **13** 1993–2002

Tansley B W, Boynton R M, 1976 "A line, not a space, represents visual distinctness of borders formed by different colors" *Science* **191** 954–957

West M, Spillmann L, Cavanagh P, Mollon J, Hamlin S, 1996 "Susanne Liebmann in the critical zone" *Perception* **25** 1451–1495