

# 27. The relative salience of the cardinal axes of colour space in normal and anomalous trichromats

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## Abstract

By imposing rival perceptual organizations on a regular spatial array, we have measured the relative salience of colour differences along the two cardinal axes of colour space. Results are reported for normal and anomalous trichromats. For most, but not all, anomalous trichromats S cone modulations are relatively more salient than they are for normal trichromats. The spatial separation of the elements of the array has a major effect on its perceptual organization.

## Introduction

One important role of colour vision is to segregate the visual field. Pseudoisochromatic plates such as those of Ishihara plainly demonstrate the power of colour to impose organization on a stimulus array: the digits in these plates are composed of discrete patches of varying lightness, and can be identified only by the hue that is common to their component parts.

Accumulated evidence suggests that our colour vision depends upon two subsystems, which evolved at different times and for different purposes. The ancient mammalian subsystem of colour vision compares the signal of the short wavelength cones with some combined signal of the long and middle wavelength cones, whereas the phylogenetically recent subsystem compares the signals of the long and the middle wavelength cones (Gouras, 1984; Mollon and Jordan, 1988; Mollon, 1991). The question of the relative roles of the two subsystems in perceptual segregation is largely unexplored.

In the normal observer, the two subsystems correspond to the two axes of the chromaticity diagram of MacLeod and Boynton (1979): at equiluminance, variations along the ordinate correspond only to variations in the short wavelength cone signal, whereas variations along the abscissa correspond to changes in the ratio of long- and middle-wavelength signals. It is convenient to refer to these 'cardinal directions' (Krauskopf *et al.*, 1982) as the S (or tritan) and the L-M (or constant-blue) axes, respectively.

Our experiments were designed to measure the relative organizing power of the signals of the two subsystems. The principle was to pit the organizing effect

of a fixed colour difference along one cardinal direction against that of a variable colour difference along the other axis. By a staircase procedure, the magnitude of the variable colour difference was adjusted so as to estimate the point at which each subsystem determined the reported organization on an equal number of trials. The method is conceptually not unlike that of Hochberg and Silverstein (1956) or Ben-Av and Sagi (1995), who pit the proximity of stimulus elements against other perceptual dimensions.

We have also applied this technique to anomalous trichromats. Although the Rayleigh matches of anomalous observers have been studied extensively, only occasional studies have attempted to penetrate the suprathreshold world of the anomal (Müller *et al.*, 1991). A natural expectation might be that a given red–green variation would be much less salient, i.e. it would enjoy less organizing power for the anomal than for the normal: the anomal is commonly thought to depend for his residual red–green discrimination on two photopigments that have very similar spectral sensitivities and these can offer only a limited range of difference signals to any channel that compares their outputs. There is, however, a plausible alternative to this prediction. During development, or indeed by relatively short-term adaptation, the dynamic range of each colour channel may match itself to the range of chromaticities in the subject's visual world. In the case of the anomal, the signals in his residual long/middle wavelength channel might expand to fill the neural space available. A process of this kind known as 'contrast adaptation' is, in fact, known to occur in the colour-normal observer (Webster and Mollon, 1995): a given colour modulation will look more salient if the observer has adapted to an array in which there are only small modulations on that axis. Laughlin (1994) has discussed the biological utility of matching the dynamic range of visual neurons to the range of contrasts available in natural scenes.

In order to compare normal trichromats and anomalous trichromats in their response to external stimuli, we have used the same stimulus dimensions for both. Since the colour matching functions of anomals differ from those of normals, the MacLeod-Boynton chromaticity diagram is not valid for anomalous observers. Moreover, there is probably a range of anomalous phenotypes (Regan *et al.*, 1994). Our unpublished calculations suggest that modulations along the S axis for normals also very nearly isolate the short wavelength cone signal for anomalous trichromats, whereas modulations along the L-M axis of normal trichromats may introduce some additional modulation of the short wavelength signal (when our stimuli are equated in luminosity for the anomal). Therefore, in discussing the results of anomalous trichromats below, we use the term 'red–green modulation' to make it clear that we refer to the external stimulus.

### **Design and stimuli**

The stimulus consisted of small circles,  $0.21^\circ$  in diameter, presented on a

graphics monitor (Sony GDM-1936), and arranged so that their nearest neighbours lay along diagonal lines (Fig. 1, right). The mean chromaticity of the circles was fixed, at Illuminant E ( $x, y = 0.333, 0.333$ ), but the colour along one diagonal of the array was modulated along the S cone axis, and along the other was modulated along the L-M axis of colour space. Thus, the two chromatic modulations imposed on the array suggest alternative perceptual organizations. The subject saw a Gestalt of diagonal lines orthogonal to the direction of the more salient modulation. On each trial he or she was asked to indicate, by pressing one of two buttons, whether the predominant organization was from upper left to lower right or upper right to lower left. The computer program randomly paired the directions of chromatic modulation with the two spatial organizations.

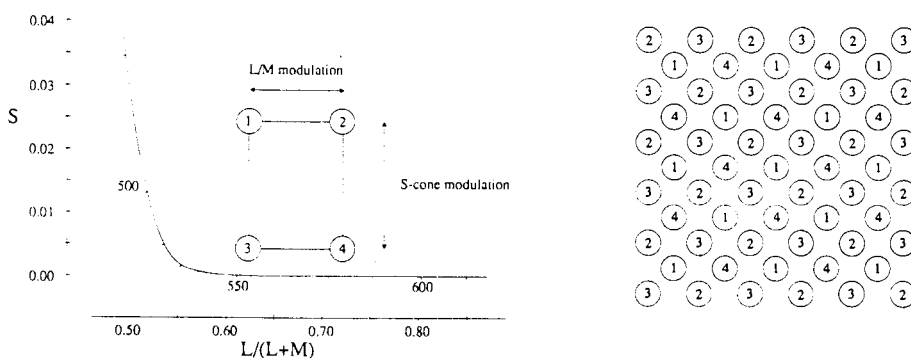


Fig. 1. To the right is shown the spatial arrangement of four chromaticities in our stimulus array. To the left are shown the positions of the four chromaticities in the MacLeod-Boynton chromaticity diagram. In this example the S cone signal is modulated along a diagonal from bottom left to top right in the array and the L/M signal is modulated along the opposite diagonal.

To ensure that the perceptual organization was driven by chromatic modulation and not luminance modulation, we varied randomly the luminances of the elements in the array, so that the maximum luminance was 1.6 times the minimum. In the case of all protanomalous and all but two deuteranomalous subjects, we additionally adjusted the mean luminances of the stimuli to allow for the altered spectral sensitivity functions of anomalous trichromats. These equations were obtained for each subject before the experiment began, using heterochromatic flicker photometry on the same monitor. For normal subjects, this procedure was not performed, and the mean luminances of differently coloured stimuli were held constant.

Chromatic modulations were computed, and are reported, in the units of the MacLeod-Boynton chromaticity diagram. Along each cardinal axis we chose

five fixed modulations. For each we adjusted the variable colour modulation along the other axis, using a staircase procedure, so that the competing modulations were each equally likely to determine the organization of the array. The ten staircases used were randomly intermingled in each block of trials. Subjects repeated the staircases several times over a number of days, and the decisions made by the subjects on every trial on each repetition of a particular staircase were combined to produce a psychometric function: the probability of the variable modulation imposing perceptual organization was plotted against the depth of that modulation. Cumulative normal distribution curves were fitted to these functions and were used to estimate the depth of the variable modulation that was equal in salience to a given fixed modulation on the other cardinal axis.

We repeated the measurements for different centre-to-centre separations of the array elements, from  $0.21^\circ$  to  $1.0^\circ$  of visual angle. Initial results showed little effect of spatial separation beyond about  $0.40^\circ$ ; therefore some of the subjects were not tested with separations greater than this.

## Subjects

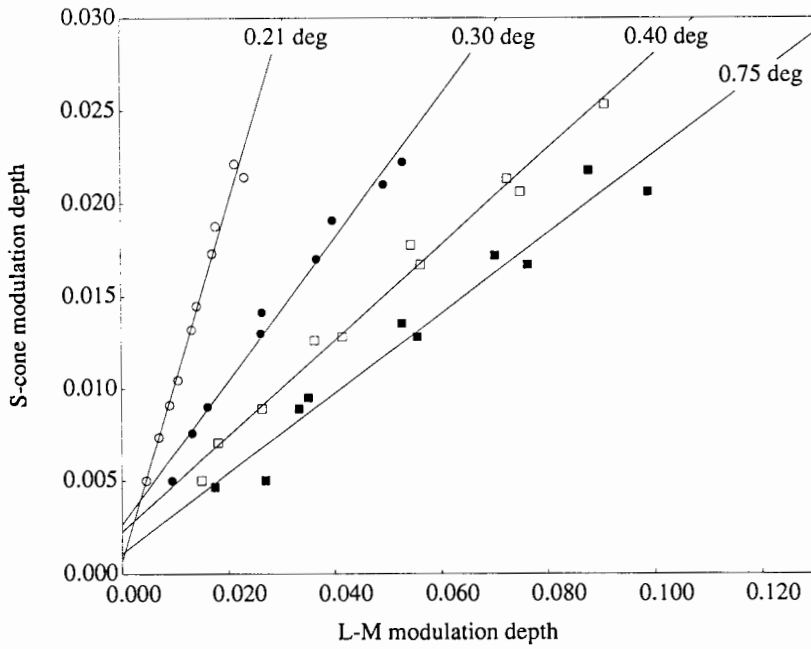
Of the 20 subjects in this experiment, three were normal trichromats (ages 20, 23 and 50 years), five were simple protanomalous (ages 14–25, mean 21.0 years) and 12 were simple deuteranomalous (ages 15–29, mean 21.25 years). Colour vision was diagnosed with the Nagel anomaloscope (model I, Schmidt and Haensch). Subjects were also tested on the Ishihara plates (10th edition) under the Illuminant C of a Macbeth easel lamp.

## Results and discussion

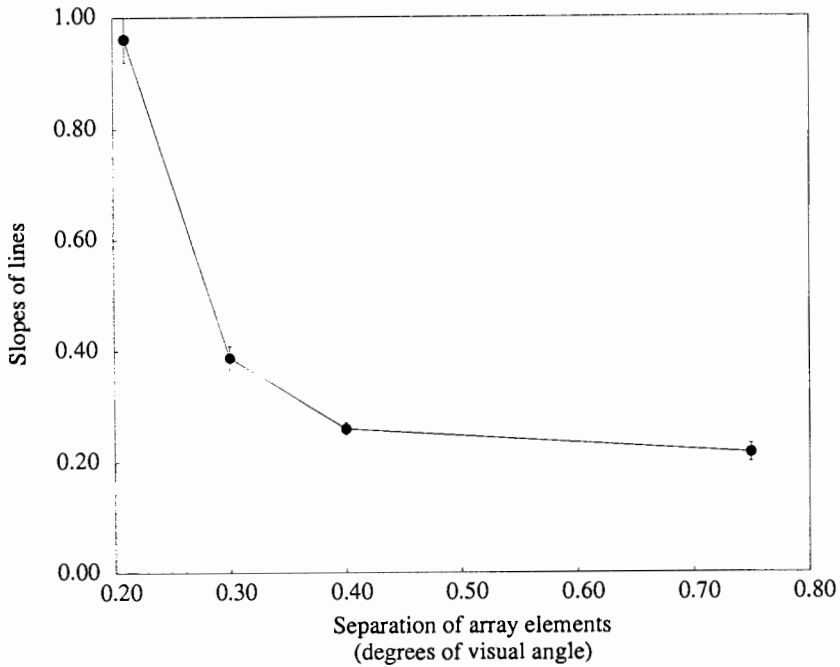
Figure 2a shows results for a normal trichromat. Each subset of data points corresponds to a particular separation of the elements in the array, and each individual point shows the depth of modulation on one axis of colour space that has the same perceptual salience as a particular modulation on the other axis. We have fitted regression lines through each subset of points, indicating the locus of equal organizing power for modulations along the two cardinal axes. The data seem to be fitted quite well by straight lines. This is a curious result, for there is much evidence that the signals of chromatically opponent channels are increasingly compressed as they depart from an equilibrium value (e.g. Le

*Figs. 2–4.* The upper graph in each pair shows the loci of equal organizing power for modulations along the two cardinal axes, at different spatial separations of the elements in the array. The lower graph shows the slopes of these loci plotted as a function of the separation of the elements in the array. The units are those of the MacLeod-Boynton chromaticity diagram. Note that the ordinate scale in Figures 3a and 4a differs from that of Figure 2a.

## Subject ELD - Normal trichromat



(a)



(b)

Fig. 2

Grand, 1949; Stiles, 1972; Polden and Mollon, 1980; Mollon and Estévez, 1988). Our data suggest either that there is a concomitant and equal compression of the signals of the two subsystems, or that the chromaticities we used were not saturated enough to drive the chromatic channels into non-linear regions of their response ranges.

A second feature of Figure 2a is that the slopes of the lines decrease as the separation of the array elements increases. In Figure 2b these slopes are plotted as a function of the separation of the array elements. The slope at  $0.21^\circ$  of visual angle is over four times as great as at  $0.75^\circ$ , indicating that the relative salience of a given S cone modulation is more than four times greater at  $0.75^\circ$  than at  $0.21^\circ$ . This may be due to (i) the low spatial resolution of the S cone system (Stiles, 1949), which must be constrained by the sparsity of the corresponding receptors (Mollon and Bowmaker, 1992), and (ii) to chromatic aberration, which would tend to blur S cone modulation more than L-M modulation. There are implications here for the construction of perceptually uniform colour spaces: such a space can be valid only for a specified spatial configuration.

Figures 3a and 3b show corresponding results for a typical protanomalous subject, and Figures 4a and 4b for a deuteranomalous subject. The S cone axis has been scaled by a factor of three in Figures 3a and 4a in order to present the results more clearly. The data still show the same effect of increasing the separation of the array elements. However, the slopes of all the lines are much less than for the normal subjects, showing that for these subjects, red-green modulation is much less salient relative to S cone modulation than for normal trichromats. For all but two anomalous trichromats in our sample, the relative salience of red-green modulation was reduced. One exception was a simple deuteranomalous subject whose results were similar to those of the normal trichromats. His setting on the Nagel anomaloscope was 18.5 units with a matching range of 2 units, but he misread only three of the Ishihara plates and obtained a 'superior normal' score on the Farnsworth-Munsell 100-hue test. A second deuteranomalous subject resembled normals at small separations, but gave greater weighting to the S cone signal at larger separations.

Figure 5 summarizes the results from all the subjects. Amongst normal trichromats, there was a two-fold variation in the locus of equal salience of modulations on the two cardinal axes, a result that has a further implication for perceptually uniform colour spaces: such spaces will not necessarily be uniform for all normal observers. Among anomalous trichromats, there is a contrast between the one or two subjects whose results are similar to normal, and the majority, for whom the salience of red-green modulation relative to the S cone modulation is much reduced.

We mentioned above the Ishihara plates as an example of the importance of colour in perceptual segregation. It is a feature of this test that eight of the plates are so-called transformation plates: they do not test directly the threshold for chromatic discrimination, but use a different stratagem, offering two alternative readings of the numbers (Lakowski, 1969). In the normal reading of these plates, the digit is distinguished from the background by a red-green difference,

## Subject IJ - Simple protanomalous

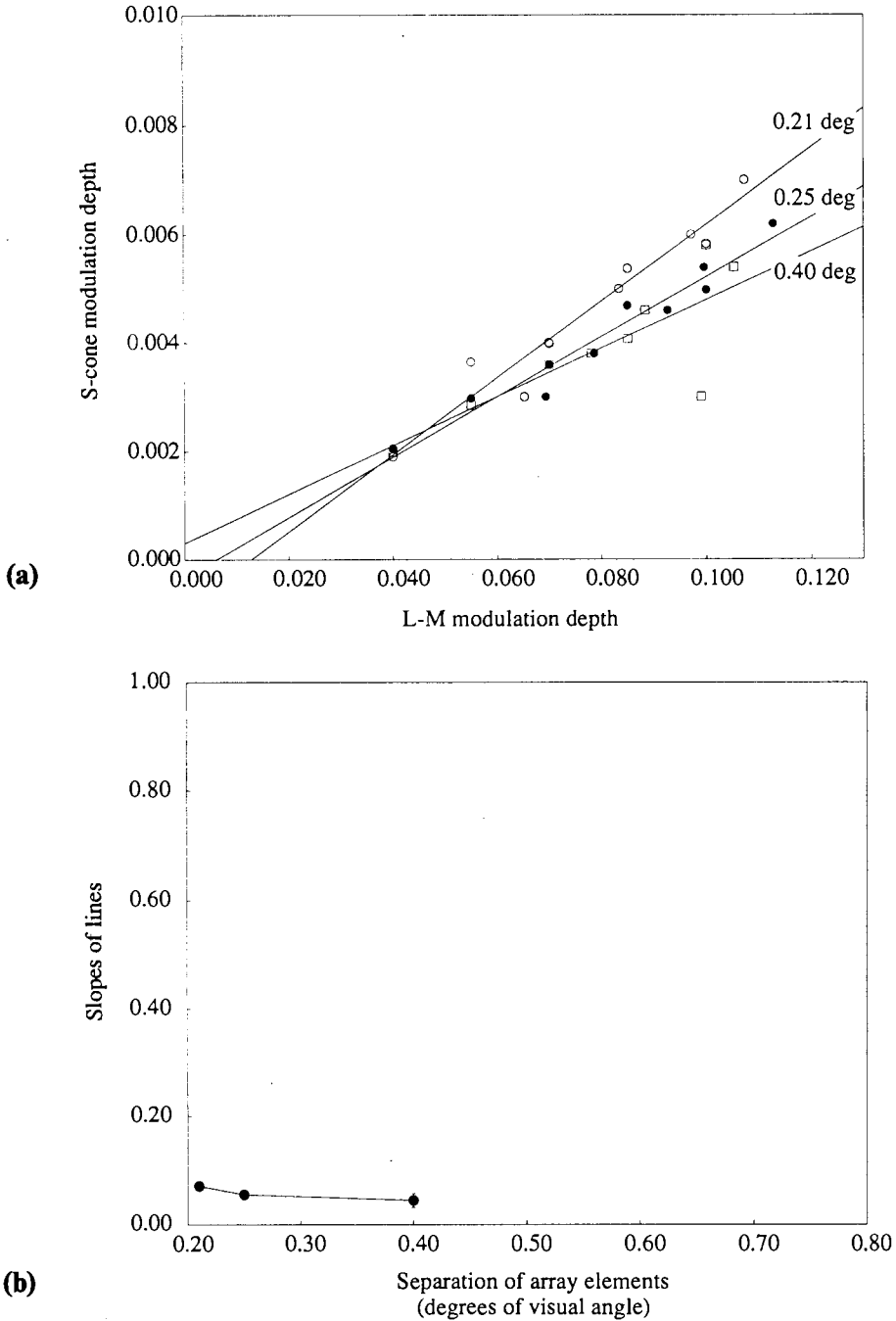


Fig.3. (see legend for Figure 2).

Subject BK - Simple deuteranomalous

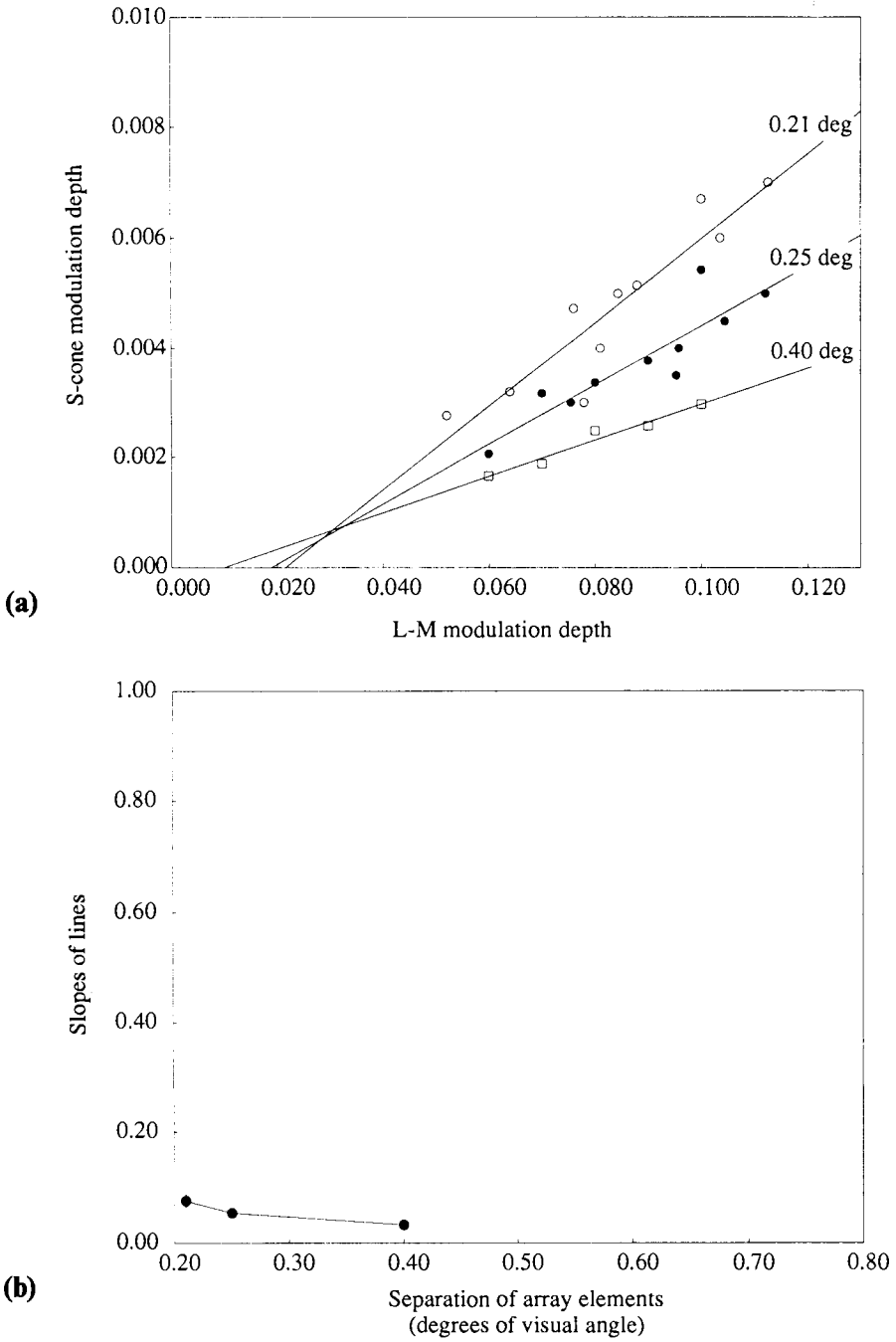


Fig. 4. (see legend for Figure 2).



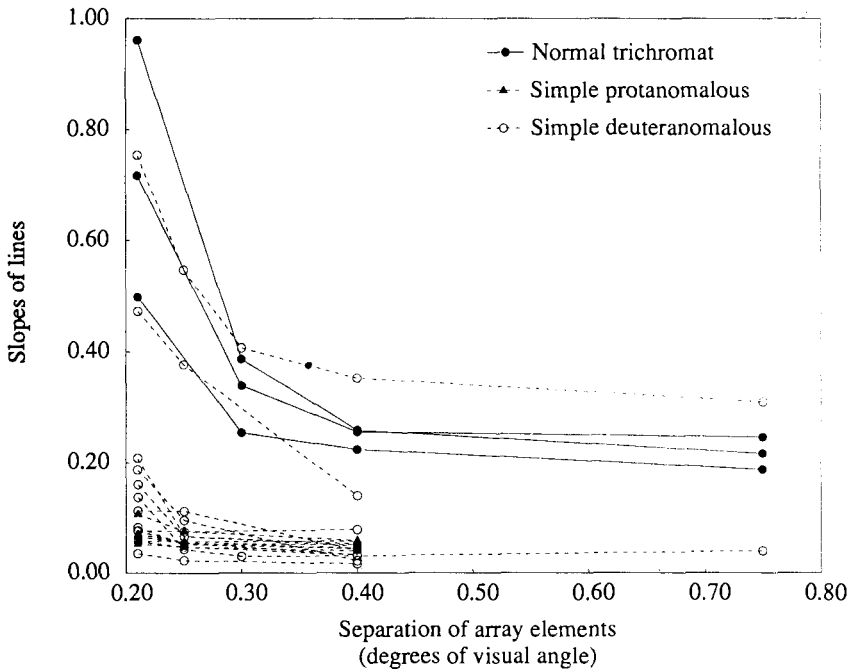


Fig. 5. Combined results from all the subjects in our sample. The slopes of the loci of equal power of the two cardinal axes are plotted as a function of the separation of the elements in the array.

whereas in the reading favoured by most anomalous trichromats the digit differs from the background in S cone excitation. It would appear that these plates depend upon the salience of the S cone difference being greater than the red-green difference for anomalous trichromats, but not for normal individuals (Reffin *et al.*, 1991). If this is the case, then for each anomalous trichromat, the relative salience of the two cardinal axes of colour space should be related to the number of misreadings made in the Ishihara transformation plates. In our sample of anomalous trichromats we found a significant correlation between the relative salience of red-green modulation and the number of Ishihara transformation plates passed. This was true for all spatial separations of the array. (With a sample size of 17, the Spearman rank order correlation coefficient was 0.456, 0.625, and 0.622 for 0.21°, 0.25° and 0.40° centre-to-centre separation of the elements in the array, significant at the 5%, 0.5% and 0.5% levels, respectively.) However, two of these eight plates were misread even by the deuteranomalous subject who resembled the normals at all separations. The broad-band stimuli of the pigments in the Ishihara plates may provide a weaker red-green signal for anomalous trichromats than the relatively narrow-band stimuli of television phosphors.

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