
Colour pools, brightness pools, assimilation, and the spatial resolving power of the human colour-vision system

Bernard Moulden

Department of Psychology, University of Western Australia, Nedlands, WA 6009, Australia

Fred Kingdom

McGill Vision Research Centre, 687 Pine Avenue West, H4-14, Montreal, Quebec H3A 1A1, Canada

Brian Wink

Department of Psychology, University of Reading, Reading RG6 2AL, UK

Received 25 January 1992, in revised form 20 June 1992

Abstract. A stimulus is described that demonstrates the spatial pooling of colour information in the visual system. Chequerboards (or gratings) consisting of alternating squares (or stripes) of complementary colours become achromatic at particular spatial scales; such stimuli have been named 'transchromatic' stimuli. Colour pools are much larger than the receptive fields that respond to luminance contrast. Some measurements are described which form the basis for estimates of the size of the colour pools. The size of colour pools varies according to the colours involved. For red-cyan and green-magenta complementary pairs colour is pooled at spatial frequencies above about 7–8 cycles deg^{-1} , implying pools whose diameter is around 8 min arc. For yellow-blue complementary pairs the corresponding figures are about 4 cycles deg^{-1} and 15 min arc. Some phenomena of normal colour vision, colour blindness, and the development of infant vision are discussed in the light of these findings.

1 Introduction

The purpose of this communication is to describe a very robust and simple demonstration of the different spatial-resolution limits for luminance and colour contrast, and to report some preliminary quantitative measurements that provoke intriguing and potentially informative comparisons with data gathered by means of more conventional techniques.

During the preparation of this communication we found that we were the reinventors, not the originators, of this demonstration. It was discovered by Hartridge (1947) who refers "... to the fact that yellow and blue test objects in close apposition, tend to decolorize one another. This was particularly noticed in the case of a grating consisting of alternate blue and yellow bars, which [became] black and white. But a similar observation was also made in the case of a grating with bars of red and blue-green, which also became black and white" (page 662).

The demonstration depends upon the use of colour pairs that are complementary—that is, the stimulus resulting from their additive mixture is achromatic, or very nearly so. For reasons of technical simplicity we chose to use the three pairs blue-yellow, red-cyan, and green-magenta. In one version, the demonstration consists of a chequerboard composed of alternating squares of complementary colours (one-dimensional square-wave gratings are equally effective). At relatively close viewing distances, each of the chequerboards appears in its full normal colour; but as one moves away from the display the chequerboards suddenly and completely lose their colour and look like high-contrast black-and-white chequerboards. A dramatic feature of the phenomenon is that moving back towards the screen by just a few centimetres restores the appearance of colour: an increase in the spatial frequency of the stimulus by just a few percent is sufficient to change the percept from 'clearly chromatic' to 'completely achromatic'.

The second significant observation is that the absolute distance (and therefore the critical spatial scale) at which the transition occurs depends upon which complementary pair is employed. The blue–yellow pair becomes achromatic much earlier (at a coarser spatial scale) than either the red–cyan or the green–magenta pair.

There is now good evidence to suggest that the mechanisms involved in signalling spatial luminance contrast are not all functionally identical with the mechanisms signalling spatial colour contrast. Some of the most persuasive formal experimental findings showing the functional separability of mechanisms responsive to different visual properties involve the use of isoluminant stimuli. A commonly used stimulus is the one-dimensional grating which varies sinusoidally in colour along the axis of modulation, with no modulation in luminance contrast. There is both electrophysiological and psychophysical evidence that suggests that information about colour and information about fine detail are carried by separable subclasses of mechanism.

For example, both Kulikowski (1991) and R L DeValois (1991) have shown that those cortical neurones which respond to high-spatial-frequency luminance contrasts tend not to be selective with respect to colour, while colour-selective cells tend to have larger receptive fields and to respond only to low spatial frequencies.

Psychophysical studies of human visual performance have shown that colour contrast sensitivity functions (CSFs) measured with isoluminant stimuli are markedly different from the corresponding luminance CSFs. The CSFs for colour, unlike those for luminance, show no low-spatial-frequency cutoff, having a low-pass rather than a band-pass characteristic. Both functions demonstrate a high-frequency cutoff, but this is at a much lower spatial frequency for colour contrast (around 12 cycles deg^{-1}) than for luminance contrast (where the limiting value is around 30–40 cycles deg^{-1}) at comparable luminance levels (for example, see Schade 1958; van der Horst and Bouman 1969; Granger and Heurtley 1973; Kelly 1973; and Mullen 1985, figure 8 and pages 392–394).

These are important and compelling findings, but they are not easy to demonstrate convincingly. It is technically not easy to produce the appropriate stimulus conditions, nor to eliminate the many sources of artifact (such as the luminance artifact that can be introduced by transverse or longitudinal chromatic aberrations of focus). One advantage of the technique described here is that the problems associated with producing stimuli that are isoluminant (which involves tailoring the chromatic parameters to suit individual subjects) and with eliminating luminance artifacts, such as those introduced by chromatic aberrations, do not arise: indeed, it is central to the demonstration that the stimuli should not be isoluminant.

Although the important qualitative features of the demonstration were clear from inspection, we wished to determine more precisely the transitional dimensions involved, and to discover the degree of similarity in these dimensions between observers. We therefore conducted an informal experiment which is described below.

2 Stimuli and method

Stimuli were generated on a 1084S monitor driven by an Amiga A500 computer with the use of a drawing package called Dpaint III. For our demonstrations and measurements we used three complementary pairs, all generated by driving the three guns R, G, B, at their maximum calibrated output. The three pairs were thus:

- red–cyan (R_{\max} versus $G_{\max} + B_{\max}$),
- blue–yellow (B_{\max} versus $R_{\max} + G_{\max}$),
- green–magenta (G_{\max} versus $R_{\max} + B_{\max}$).

We particularly chose to use complementary colours, for two reasons. First, the mean luminance of all our displays was necessarily constant. This is because in each case the stimuli were produced by driving all three guns at maximum; the only thing that

differed from condition to condition was the distribution of the illuminated coloured pixels, not their number or their intensity. Second, as described earlier, the change in appearance of the displays is categorical, from being a two-coloured chequerboard to being a black-and-white one, compared with the change from being a red-green grating, say, to being a yellow homogeneous patch. The change in appearance from chromatic to achromatic is not only more compelling but also subjectively more definite than the change merely from heterochromatic to homochromatic. For convenience, we refer to a stimulus consisting of complementary colour pairs in equal spatial proportions as a 'transchromatic' stimulus, reflecting the fact that at a particular spatial scale such a stimulus changes from being chromatic to being achromatic.⁽¹⁾

Three transchromatic chequerboard patterns were generated, each containing one of the three complementary pairs. With the aid of the 'magnify' facility of the software package, the size of the squares making up the chequerboards could be scaled as required. The width of the individual squares was measured with a travelling microscope. The edges of the display were masked with tracing paper so that only a 10 cm diameter circular region was left clear.

With the subject located approximately 2 m from the display, the spatial scale of the chequerboards was varied by the experimenter, partly to demonstrate the nature of the observation to be made and partly to establish a starting point for those observations. Subjects were then required to move slowly towards or away from the screen and to report the point at which the chequerboard appeared to be "just black and white, with no colour". A measuring tape attached to the wall permitted the experimenter to read off the distance of the subject from the display at that point, and

Table 1. Spatial scale of the chequerboard (in cycles deg⁻¹) at which the chequerboard containing a complementary colour pair appeared achromatic to nine subjects.

Subject	Complementary pair		
	blue-yellow	red-cyan	green-magenta
1	3.85	7.32	6.99
2	4.17	5.74	5.26
3	3.04	6.90	6.67
4	3.90	10.14	8.68
5	4.82	9.27	9.65
6	3.34	6.93	6.99
7	6.48	13.09	9.82
8	3.40	6.32	5.94
9	3.45	6.13	6.65
Mean	4.05	7.98	7.40
SD	0.99	2.27	1.44

⁽¹⁾ After we had carried out the informal experiment to be described, we developed a refinement of the demonstration. This consisted of a 10×10 transchromatic chequerboard embedded in a 30×30 achromatic chequerboard surround. It proved to be a simple matter to adjust the luminance of the light and dark achromatic squares by trial and error so that both the mean luminance and the contrast of the surround perfectly matched those of the coloured chequerboard when the latter appeared achromatic. The match can be made so precisely that it is not possible to discriminate between two stimuli, one of which consists throughout of achromatic squares and the other of which contains an embedded transchromatic chequerboard. This means that in principle the spatial limits of the effect could, if required, be investigated by means of a two-alternative forced-choice procedure. However, for our purposes this procedural refinement was unnecessary and we used what was effectively a method of adjustment.

this constituted the datum. Several (between two and six, according to the time available) such measurements were taken for each subject for each of the three gratings. These distance measurements were then converted into cycles deg^{-1} , where one cycle is defined as one pair of chequerboard squares.

3 Results

The results obtained (cycles per deg^{-1}) from nine subjects are shown in table 1.

4 Discussion

A notable feature of the transchromatic stimulus is the sharpness of the transition in its appearance from chromatic to achromatic: the average standard deviation of the individual settings for the blue-yellow condition was 0.3 cycle deg^{-1} . This may be interpreted as demonstrating that the colour system has a very high gain under these conditions: that is, the output of the colour system changes rapidly from zero to high in response to very small changes in the input conditions over a certain critical spatial range. This is a striking demonstration of the steepness of the high-frequency cutoff aspect of the spatial-frequency response of the chromatic system. It is generally accepted that the high-frequency limit (at around 60 cycles deg^{-1}) in the luminance-contrast domain is not explicable in terms of the limiting optics of the eye (Campbell and Green 1965; Jennings and Charman 1981), and is assumed to reflect the sampling limits of receptive field spacing. It is plausible to suppose that the high-frequency cutoff in the colour domain (at around one quarter or one eighth of the luminance contrast value, depending upon the absolute luminance) similarly represents not optical factors but rather the sampling limits set by receptive fields that pool colour information.

The mean transchromatic point for the blue-yellow stimulus was at a spatial frequency of 4.05 cycles deg^{-1} ; for the red-cyan pair it was at 7.98 cycles deg^{-1} ; and for the green-magenta pair it was at 7.40 cycles deg^{-1} . The similarity of the pattern of results across subjects (with the possible exception of the red-cyan value for subject 7) confirms the generality of the phenomenon and indicates that individual differences are small. [With subject 7 removed, the standard deviations (in cycles deg^{-1}) are: blue-yellow, 0.45; red-cyan, 1.56; green-magenta, 1.42.] The most marked features of these results are, first, the similarity of the data from the red-cyan chequerboard and those from the green-magenta display, and second, the equally marked difference between each of these and the results for the blue-yellow chequerboard. For the latter, colour is undetectable even when the squares are almost twice the size at which the green-magenta and red-cyan chequerboards retain their colour.

These results imply not only that the area over which colour is pooled is larger than the area over which luminance is pooled, but, further, that at some level of the system the area over which colour information is pooled is much larger for mechanisms signalling blue-yellow colour contrast than it is for those signalling green-magenta or red-cyan contrast.

One alternative explanation might be that in some sense the effective colour contrast of the blue-yellow combination is less than that of the other two combinations. If this were to be so the magnitude of the internal signal describing the colour difference between adjacent elements would be smaller and might be expected to disappear below threshold earlier under adverse conditions such as relatively high spatial frequency. This is unlikely, since the blue-yellow pattern has a higher apparent contrast than the other two, not a lower one.

However, it is possible that the apparently higher contrast of the blue-yellow combination could have been due to higher brightness contrast, rather than higher chromatic contrast. When the three stimuli were compared, at a viewing distance at

which all three colour pairs appeared achromatic, the blue–yellow stimulus did indeed appear to be of higher brightness contrast. This left open the possibility that the chromatic contrast of the blue–yellow pair was in fact lower than that of the other two pairs of colours.

To investigate this possibility we altered the chromatic contrast of each of the three stimuli. If the difference between the blue–yellow combination and the other pairs was due to differences in the effective colour contrast, then manipulating the colour contrast should cause a shift in the transition point. This was done by desaturating each of the colours (that is, for example, by adding equal amounts of red and green to the blue squares, and blue to the yellow squares). This makes the colours more similar to each other, and thus the chromatic contrast is reduced (taking the procedure to its extreme would cause both blue and yellow to become white—zero colour contrast).

This manipulation did not change the transition point of any of the three colour pairs. The colour still vanished at the same spatial scale. Thus differences in the effective colour contrast do not appear to provide a convincing explanation for the difference in transition point for the blue–yellow combination and the other two combinations.

We do not believe that either transverse or longitudinal chromatic aberration can be playing a major part in this effect. First, the introduction of artificial blur, either by viewing through inappropriate spectacle lenses or by removing one's normal correcting lenses, makes virtually no difference to the location of the transchromatic transition point. Second, the results are just the same when the observations are repeated with a 2 mm artificial pupil. Hartridge (1947) reached the same conclusions: "That this hypothesis [concerning the role of chromatic aberration] is unlikely, or at least does not play the part preliminarily assigned to it, is clearly proved by the tests described above, in which the diameter of the pupil, and, therefore, the diameters of the aberration disks, were altered in the ratio of more than 3 to 1, without an observable effect on the visual angle at which colour loss occurred. This conclusion was confirmed by other experiments, in which the chromatic aberration of the eye was corrected by means of a suitable crown-flint glass combination" (page 552).⁽²⁾

At first sight our suggestion that the functional pooling area for blue–yellow is larger than that for either of the other two complementary pairs might seem to be inconsistent with data describing the limited acuities for chromatic gratings. Mullen (1985) has shown that red–green and blue–yellow isoluminant modulations appear to support very similar limiting acuities, at around 11 or 12 cycles deg^{-1} . Leaving aside the probably minor difference that we paired cyan (B + G)—rather than just green—with red, there is still no necessary inconsistency.

It is possible that our results represent genuine estimates of the size of what we choose to refer to as 'colour pools' while the 'isoluminant CSF' data do not. In the observations reported here the dependent variable is explicitly the perceived chroma of the stimulus, rather than the perceived spatial structure as in the chromatic CSF experiments. Despite the care taken by Mullen (1985) to try to eliminate the possibility, it is still possible that the higher-frequency cutoff point she reported might be due

⁽²⁾ Indeed, Hartridge was led to propose that the phenomenon reflected the operation of a mechanism whose function was to ameliorate the effects of chromatic aberration: "Of the various hypotheses advanced to explain the colour changes described ... only one fits in with the observed facts, namely, that there is a neurological mechanism situated somewhere on the nerve path between the photoreceptors of the retina, and the brain; this consists of four separate parts, one for blue, one for yellow, one for red, and one for blue–green: these are responsible for bringing about the colour changes, and are therefore responsible for eliminating the fringes produced by the chromatic aberration of the lens system of the eye. For this reason they have been called the 'antichromatic responses'" (Hartridge 1947, page 566).

to some residual luminance contrast artifact. There are at least two possibilities in this regard, one optical, straightforward, and dull, while the other is biophysical, more complex, and intriguing.

The first possibility is simply that, despite whatever steps one might take, there may be some irreducible degree of chromatic aberration. As a result of differential effects on the location and the magnification of different-wavelength components of heterochromatic images (see Thibos et al 1990, for example) this will introduce unwanted physical luminance contrast in the retinal image.

The second and more interesting possibility is that the unwanted luminance contrast signal could be due to neural, not physical, factors. It is possible that labelled colour-pooling receptive fields are large and unable to resolve chromatic spatial modulation above some limiting spatial frequency—perhaps around 4 to 7 cycles deg^{-1} . The higher resolution limit reported by Mullen might not reflect the operation of units capable of supporting hue discrimination, but rather of smaller-field units whose job it is simply to describe spatial modulation. If, as seems certain, these units (or even only some of them) were unbalanced in their chromatic opponency then they would give an output to the isoluminant stimulus. That output would be unlabelled with respect to colour information, and the signal would be indistinguishable from one developed in response to a luminance modulation. Because the effective luminance contrast developed in this way would necessarily be limited in amplitude, and since the magnitude of even this limited signal would vary probabilistically according to the randomly determined chromatic balance of each cell, the total effective signal in response to an isoluminant stimulus would be equivalent to a luminance contrast of very small amplitude. The resolution limit would be correspondingly low compared with the resolution possible with high physical contrasts, but nevertheless high compared with the performance limits of the labelled chromatic units. According to this argument, what Mullen has called ‘chromatic summation areas’ (Mullen 1991) and what we call here ‘colour pools’ may be, although they are not necessarily, functionally quite distinct entities. The measurement of the limits of spatial resolution with the use of coloured stimuli may be an entirely appropriate way to describe ‘chromatic summation areas’. Yet it might be mistaken to conclude that the spatial limits of ‘chromatic summation areas’ measured in this way genuinely reflect the spatial colour-resolving limits of the system.

We argue that the functional size of colour pools should properly be described by measuring spatial limits of colour resolution, just as was originally done by Hartridge (1947), Granger and Heurtley (1973), van der Horst et al (1967), and van der Horst and Bouman (1969).

The general notion that there exist ‘brightness pools’ and ‘colour pools’ and that these are larger than ‘luminance-contrast pools’ helps to refine our understanding of the visual mechanisms underlying such techniques of painting as pointillisme. This is usually explained by reference to the following class of demonstration, which is frequently also used to illustrate additive colour mixing. A patch consisting of very small randomly intermixed dots, some red and some green, is seen veridically at close viewing distances. At much longer viewing distances, when the individual dots are not resolvable, the colours are physically mixed on the retina because of the overlapping blur circles of the individual dots. The subtle gradations of colour achieved by the pointilliste technique are explained by extension: the individual points of colour are similarly physically mixed by optical blur. For a demonstration of the effect and a particularly clear statement of this view (“... Seurat ... allowed the mixture to be accomplished optically within the eye...”) see Coren et al (1984), page 184. This explanation quite overlooks the fact that the subtle colour gradients are still perfectly visible, as is the additive mixture of red and green dots, at a spatial scale where the

individual dots (though not their hues) are still resolvable, so that the account in terms of physical blur is clearly inapplicable. The blending occurs, we argue, not because of physical blurring but rather because of the 'neural blurring' that is a consequence of the operation of the kinds of 'colour pools' that have been discussed in this paper.

Exactly the same kind of reasoning applies in the brightness domain. In the case of halftone monochrome print images there exists a scale at which the dot structure of the halftone screen is still resolvable, but the brightness of regions in the image, which is carried by the density of the dots, is also independently available. The same effect is observable in prints produced by certain engraving techniques, particularly woodcuts. Narrowly spaced but clearly resolvable ink lines on white paper make the white space in the hatched area look darker than the white substrate appears in broad unhatched areas (see Goldstein 1989, page 153 for an excellent example). Why should the substrate of hatched regions look illusorily dark? It is difficult to escape the conclusion that this is yet another manifestation of some kind of spatial averaging of luminance information by 'brightness pools'. Such an idea was proposed by Jameson and Hurvich (1975).

A similar explanation may be offered for the formal demonstration originally described by Bezold (1876) which was called by him the 'spreading effect' and which has come to be known as 'assimilation'. Such demonstrations frequently involve coloured substrates, but most involve an effect only upon the brightness, not the perceived hue, of that substrate. A dark filigree pattern overlaid upon a patch of colour makes the colour look darker in shade; a light filigree makes it look lighter. An example is given by Goldstein (1989; colour plate 5.3), and an achromatic example is given by Coren et al (1984, page 161). In terms of the general approach adopted in this paper, the 'spreading effect', or brightness assimilation, would be interpreted as indicating that there are pools for brightness which are spatially more extensive than the receptive fields that underlie spatial resolution of fine detail on the basis of luminance contrast (Jameson and Hurvich 1975). Interestingly, what estimates we have of the approximate limiting spatial scale of these putative 'brightness pools' suggests that they are comparable with our smallest estimates of those for colour. Both Helson (1963) and Hamada (1984) have measured the magnitude of brightness assimilation as a function of spatial frequency, and concluded that the limiting spatial frequency for achromatic assimilation effects is around 4 cycles deg^{-1} .

There also exist demonstrations of genuine 'colour assimilation' in which the hue of a chromatic homologue of a superimposed filigree or its equivalent influences the perceived hue of the background. A good example is to be found in R L DeValois and K K DeValois (1987, their figure 7.10), who refer to the phenomenon as 'colour similitude'. We interpret this as having exactly the same explanation as the transchromatic demonstration described above. In particular, we would predict that it would have similar colour-dependent spatial properties: the spatial limits for colour assimilation involving blue or yellow should be at a coarser scale than those for red, green, cyan, or magenta.

It is possible that the size of colour pools measured in the way we propose (that is, with colour as the explicit discriminandum) may reveal degrees of colour-vision anomaly in terms of subjects' spatial resolution of colour. We speculate that, rather like the way classical acuity tasks measure only the limiting high-frequency cutoff point on the luminance CSF, classical tests for colour blindness too may be limited in spatial generality. One common test for colour anomaly consists of the so-called isochromatic plates. These plates, which consist entirely of small dots or patches, contain letters or digits which are defined only by their difference in hue with respect to their background. They carry spatial information predominantly in the high frequencies.

The possibility exists that in some cases at least, the failure to resolve such stimuli might indicate not a complete absence of colour resolution, but merely, perhaps, the absence of colour pools of normal size. Subjects with abnormally large colour pools would not be able to detect the critical features in a standard test stimulus but they might still retain some residual colour discrimination which would be revealed by chromatic stimuli of sufficiently low spatial frequency. This would lead one to expect that there would be some individuals who according to standard criteria are judged to be colour blind, but who can nevertheless make rudimentary colour discriminations if the stimuli are sufficiently large. Just such a phenomenon has been described by Nagy and Boynton (1979).

Moreover, in normal subjects using the periphery of the retina the discrimination of stimuli on the basis of wavelength has been shown to be possible only with relatively large stimuli (Gordon and Abramov 1977; Noorlander et al 1983), just as one might expect if colour pools, like ganglion cell receptive fields, get larger with increasing eccentricity.

If the size of colour pools were in general to be correlated with the size of receptive fields then one might expect to find an analogous effect in the development of infant colour vision. It seems well established that luminance summation regions (and therefore by inference, receptive fields) in infants are very large compared with their adult value (see for example Hamer and Schneck 1984; Schneck et al 1984). It is therefore interesting to note that Adams et al (1990) reported that infants could only discriminate coloured patches from white when the patches were very large (many degrees in diameter). Moreover, the size required for newborns to demonstrate a discrimination varies with wavelength: red squares and green squares could be discriminated from white at a size of about 8 deg, but newborns required a 16 deg stimulus to discriminate a yellow square, and showed no evidence of discriminating a blue square even when tested with 32 deg squares. The parallel with the colour-dependency of the transchromatic demonstration described here is obvious.

References

- Adams R J, Maurer D J, Cashin H A, 1990 "Influence of stimulus size on newborns' discrimination of chromatic from achromatic stimuli" *Vision Research* **30** 2023-2030
- Bezold W von, 1876 *The Theory of Colour* American edition (Boston, MA: Prang)
- Campbell F W, Green D G, 1965 "Optical and retinal factors affecting visual resolution" *Journal of Physiology (London)* **181** 437-445
- Coren S, Porac C, Ward L M, 1984 *Sensation and Perception* second edition (New York: Academic Press)
- DeValois R L, 1991 "Orientation and spatial frequency selectivity: properties and modular organisation" in *From Pigment to Perception* Eds A Valberg, B B Lee (New York: Plenum)
- DeValois R L, DeValois K K, 1987 *Spatial Vision* (Oxford: Oxford University Press)
- Goldstein E B, 1989 *Sensation and Perception* (Belmont, CA: Wadsworth)
- Gordon J, Abramov I, 1977 "Colour vision in the peripheral retina. II Hue and saturation" *Journal of the Optical Society of America* **77** 202-207
- Granger E M, Heurtley J C, 1973 "Visual chromaticity-modulation transfer function" *Journal of the Optical Society of America* **63** 1173-1174
- Hamada J, 1984 "Lightness decrease and increase in square-wave grating" *Perception & Psychophysics* **35** 16-21
- Hamer R D, Schneck M, 1984 "Spatial summation in dark-adapted human infants" *Vision Research* **24** 77-85
- Hartridge H, 1947 "The visual perception of fine detail" *Philosophical Transactions of the Royal Society of London* **232** 519-671
- Helson H, 1963 "Studies of anomalous contrast and assimilation" *Journal of the Optical Society of America* **53** 179-184
- Horst G J C van der, Bouman M A, 1969 "Spatiotemporal chromaticity discrimination" *Journal of the Optical Society of America* **59** 1482-1488

-
- Horst G J C van der, Weert C M M de, Bouman M A, 1967 "Transfer of spatial chromaticity contrast at threshold in the human eye" *Journal of the Optical Society of America* **57** 1260-1266
- Jameson D, Hurvich L M, 1975 "From contrast to assimilation: In art and in the eye" *Leonardo* **8** 125-131
- Jennings J A M, Charman W N, 1981 "Off-axis image quality in the human eye" *Vision Research* **21** 445-455
- Kelly D H, 1973 "Lateral inhibition in human colour mechanisms" *Journal of Physiology (London)* **228** 55-68
- Kulikowski J J, 1991 "On the nature of visual evoked potentials, unit responses and psychophysics" in *From Pigment to Perception* Eds A Valberg, B B Lee (New York: Plenum)
- Mullen K T, 1985 "The contrast sensitivity of human colour vision to red-green and blue-yellow chromatic gratings" *Journal of Physiology (London)* **359** 381-409
- Mullen K T, 1991 "Colour vision as a post-receptoral specialisation of the central visual field" *Vision Research* **31** 119-130
- Nagy A L, Boynton R M, 1979 "Large-field colour naming of dichromats with rods bleached" *Journal of the Optical Society of America* **69** 1259-1265
- Noorlander C, Koenderink J J, den Ouden R J, Edens B W, 1983 "Sensitivity to spatiotemporal colour contrast in the peripheral receptive field" *Vision Research* **23** 1-11
- Schade O H, 1958 "On the quality of colour television images and the perception of colour detail" *Journal of the Society of Motion Picture and Television Engineers* **67** 801-806
- Schneck M, Hamer R, Packer O, Teller D Y, 1984 "Area-threshold relations at controlled retinal locations in 1-month old infants" *Vision Research* **24** 1753-1764
- Thibos L N, Bradley A, Still D L, Zhang X, Howarth P A, 1990 "Theory and measurement of ocular chromatic aberration" *Vision Research* **30** 33-49