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The comparison of spatially separated colours

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Abstract

We have measured chromatic discrimination as a function of the spatial separation of the stimuli within the visual field. Pairs of stimuli were presented on an imaginary circle of 5° radius and the distance between their centres was varied up to 10°. Stimulus duration was 100 ms. Constructing an analogue of the MacLeod–Boynton diagram for an extra-foveal observer, we made separate series of measurements for the $L/(L + M)$ and $S/(L + M)$ axes of colour space. For both these axes, discrimination was optimal when there was a small spatial interval between the boundaries of the stimuli; thereafter thresholds rose moderately with increasing separation. Nevertheless, even at a separation of 10°, subjects exhibited impressive discrimination, achieving thresholds in the range 0.4–2% on the $L/(L + M)$ axis and in the range 3–6% on the $S/(L + M)$ axis. Even when the two stimuli fell in different hemifields and transmission of information across the corpus callosum was required, accuracy did not differ significantly from that obtained when both stimuli fell within one hemifield. The human ability to compare remote stimuli requires an explanation. We argue that the discrimination is unlikely to depend on hard-wired neural comparators and may depend on neural representations that can be transmitted on a cerebral bus independently of the particular neurons carrying the code. Contrary to earlier reports, chromatic discrimination was not systematically better in the left visual field than in the right. And only one subject showed a significant advantage of the lower hemifield over the upper hemifield.
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1. Introduction

Colour discrimination is traditionally studied with juxtaposed stimulus fields, usually foveal but sometimes peripheral. We ask here a neglected question: How well can colours be discriminated when the discriminanda are well separated in the visual field? Does discrimination deteriorate with increasing separation? Lying behind this empirical question is a theoretical question, one that is also seldom addressed: what is the neural mechanism that allows us to compare the attributes of objects that are distant from one another in the visual field?

1.1. Colour discrimination contrasted with luminance discrimination

When subjects are asked to compare the luminances of lights or the lightnesses of surfaces, it is found that discrimination is optimal when the two fields are abutting, as in the interleaved fields of a classical photometer (Walsh, 1958, pp. 195–196) The precision of discrimination is reduced as soon as any contour is introduced between the two fields (Boynton, Hayhoe, & MacLeod, 1977; Montag, 1997; Traub & Balinkin, 1961; Whittle, 1992). Measuring the precision with which subjects could equate the luminances of 1° semicircular patches, Burgh, Grindley, and Whittle (1961) found that the scatter of settings increased markedly as the separation of the stimuli increased from 0 to 6 arcmin, but they also found that the scatter continued to increase for separations up to 4°.

Similarly, Sharpe and Wyszecki (1976) found that thresholds for luminance discrimination were two- or threefold higher for fields separated by 4.1° of visual angle than for fields separated only by 'an extremely fine' dividing line.

It is plausible to suppose that the precise discrimination of abutting luminances depends on signals deriving from hard-wired neural comparators. We could identify these dedicated comparators with centre–surround retinal ganglion cells, which are sensitive to the relative illumination falling on adjacent regions of the receptor array (Kaplan, Shapley, & Purpura, 1988; Kuffler, 1953). The difference or ratio signal transmitted to the cortex from such cells directly represents local contrast; and phenomena such as the Craik–Cornsweet illusion (Craik, 1940, p. 64) suggest that these local edge signals may determine perceived lightness over a large region. Analogous local comparators are thought to exist for several other stimulus attributes: for example, directionally selective movement detectors make a spatiotemporal comparison of the illumination falling on adjacent retinal regions (Barlow & Levick, 1965), while some cortical simple cells are particularly responsive to a discrepancy in orientation between a central and an annular grating (Sillito, Grieve, Jones, Cudeiro, & Davis, 1995). And these physiological findings are consistent with a heightened psychophysical sensitivity to local discontinuities in primitive visual features (Allman, Miezin, & McGuinness, 1985; Sagi & Julesz, 1987).

Colour, like lightness, is a local property of surfaces in the visual world. Should we expect colour discrimination to deteriorate in the same way as lightness discrimination when the discriminanda are spatially separated? The recognition of chromaticity itself depends on a first-order comparison between the signals of different classes of cone: the midget and the small bistratified ganglion cells of the primate retina draw inputs of opposite sign from different types of photoreceptor (Dacey & Lee, 1994; Gouras, 1968). Should we postulate second-order comparators that compare the first-order chromaticity signals from adjacent retinal regions? Such a role might be attributed to the double-opponent cells that have been reported at a cortical level (Conway, 2001; Johnson, Hawken, & Shapley, 2004; Michael, 1978a, 1978b, 1978c). Do such cells provide a local difference signal that is analogous to the local difference signal thought to underlie the discrimination of luminance?

In the case of colour, the existing psychophysical literature does not offer consistent guidance. From experiments with stabilised images (Ditchburn & Foley-Fisher, 1983; Krauskopf, 1963, 1967) and from the watercolour effect (Devinck, Delahunt, Hardy, Spillmann, & Werner, 2005), there is evidence that colour appearance over a large area can be influenced by the transition between chromaticities at edges. On the other hand, the chromatic analogue of the Craik–Cornsweet illusion is much weaker than its counterpart for luminance (Wachtler & Wehrhahn, 1997; Ware & Cowan, 1983). And perhaps most fundamentally, the spatial contrast sensitivity function for colour is low-pass in form and not band-pass like that for luminance (Cavonius

& Estévez, 1975). In the case of luminance, the band-pass form of the spatial CSF has traditionally been explained in terms of a range of channels with spatially opponent receptive fields: the visual system is insensitive to very low spatial frequencies because the slow variation of luminance across the retina means that the centres and surrounds of even the largest receptive fields differ little in their excitation. The absence of a similar low-frequency attenuation in the *chromatic* CSF argues that chromatic sensitivity is not limited by second-order comparators that compare the chromatic signals from adjacent regions. Another relevant literature is that on colour contrast and colour constancy: here the evidence is that colour induction declines with increasing separation between the boundaries of the inducing and test fields, but there is a residual and distinct effect on colour appearance of remote stimuli (Brenner & Cornelissen, 1991; Oyama & Hsia, 1966; Spillmann & Werner, 1996; Wachtler, Albright, & Sejnowski, 2001; Walraven, 1973; Wesner & Shevell, 1992). In the experiments of Oyama and Hsia (1966), contrast effects were still present when the test and inducing fields were separated by 8°.

With regards to our primary question—of whether colour discrimination, like luminance discrimination, deteriorates rapidly with spatial separation—there are only limited psychophysical data. In contrast to the case for luminance discrimination, the visibility of colour differences may sometimes be enhanced by the introduction of a thin gap between two equiluminous stimulus fields (Boynton et al., 1977; Malkin & Dinsdale, 1972; Montag, 1997). With respect to larger separations, Traub and Balinkin (1961) briefly report that there is little variation in the accuracy of discrimination for centrally viewed stimuli separated by distances between 0° and 0.88° of visual angle (their Fig. 8). Sharpe and Wyszecki (1976) measured difference limens for stimulus separations of 0° and 4.1°: whereas luminance limens increased two- or threefold with separation, hue thresholds rose by no more than a factor of 1.3 and were sometimes unchanged. For separations up to 0.8°, Judd (1930) found no change in the precision of colour matches if there was a light grey band between the test fields, but discrimination did deteriorate if the intervening band was black. In all these experiments, the subject was free to move his or her eyes between the stimuli and thus the discrimination could be achieved by comparing successive signals from the same channel.

1.2. Present experiments

Our purpose in the present experiments was to examine how the precision of colour discrimination varied with the spatial separation of the discriminanda. Separations of up to 10° of visual angle were tested, with eccentricity held constant. We used brief exposures to ensure that subjects could not move their eyes from one stimulus to the other but were required to compare signals deriving from different retinal regions.

We made separate measurements for the two cardinal axes of colour space (Krauskopf, Williams, & Heeley, 1982): one axis corresponds to a phylogenetically ancient channel, which compares the signal of the short-wave cones with some combination of the long- and middle-wave cones, and the second axis corresponds to the phylogenetically recent channel that compares the signals of the long- and middle-wave cones (Derrington, Krauskopf, & Lennie, 1984; Mollon, 1989). We were interested to examine separately these two chromatic subsystems, since short-wave cones are much sparser than long- and middle-wave cones in the human retina (Bowmaker, Parry, & Mollon, 2003) and long tradition holds that spatial integration is greater for the signals of the short-wave cones (Brindley, 1954; Regan & Mollon, 1997; Stiles, 1949).

1.3. Ensuring that the stimuli are actively compared

In studying any psychophysical discrimination, it is important to ensure that subjects actively compare the two discriminanda and do not simply make absolute judgements of one target stimulus (Danilova & Mollon, 2003; Lages & Treisman, 1998). Over a sequence of trials, the subject may build up an internal template, a neural representation of the average stimulus presented; and it may be against this template that the target is judged, rather than against a second external stimulus. A strategy of this kind might be efficient, because the subject's judgement is then based on only one sample of external noise, rather than the two samples of external noise that would be introduced if a comparison of the target and reference stimulus were made.

We show that subjects in the conditions of our experiment can indeed make absolute judgements with a precision similar to that of their discrimination judgements, and Morgan, Watamaniuk, and McKee (2000) have shown that subjects can maintain several absolute criteria concurrently. To ensure that our subjects do compare the two stimuli, we randomly jitter the reference stimulus from which the target must be discriminated. We take 25 finely spaced reference stimuli in a region of stimulus space where the Weber fraction is nearly constant, and thus we are able to measure thresholds with a single staircase but an unpredictable reference stimulus. Moreover, on any trial, the subject does not know which stimulus is the reference stimulus and which is the nominal target. Thus, the subject is obliged always to take both stimuli into account. In a control experiment, we show that performance is severely impaired if only one of the two stimuli is available to the subject.

2. General methods

2.1. Apparatus and stimuli

The experiments were primarily carried out in St. Petersburg, Russia, using a Sony Triniton 21-in. monitor (GDM-F500), under the control of a VSG 2/5 graphics board (Cambridge Research Systems). The refresh rate of the screen was 80 Hz. Pilot studies and the control measurements for JM and MD (Fig. 7) were carried out in Cambridge, UK, using similar programs and apparatus (GDM-F500 display, VSG 2/3 graphics board), the same calibration equipment, and a refresh rate of 100 Hz. No systematic differences were found between results measured in the two laboratories. Both VSG graphics boards allowed stimuli to be specified with a precision of 15 bits per gun.

The CRT screen was viewed binocularly from a distance of 57 cm. The stimuli to be discriminated were presented on a steady background, which had a chromaticity equal to that of equal energy white for the Stockman and Sharpe (2000) 10° observer. The discriminanda were sectors of an annulus, and their centres lay on an imaginary circle with a radius of 5° of visual angle. The imaginary circle was centred on a continuously present fixation point (see Fig. 1). The width of each target sector at its midpoint was 2° of visual angle, and its radial length was 2°. Thus, when the separation of the stimulus patches was 2° of visual angle, their edges were touching, and when their separation was 10° they lay on a diameter of the imaginary circle. On any trial, the midpoint of the two patches lay on a radius that had a random angle chosen in steps of 5°, starting from 12 o'clock. The duration of the stimulus patches was 100 ms, a duration chosen to be too short to allow eye movements between them.

2.2. Calibrations

Calibrations were performed with a Spectrascan 650 spectroradiometer. To calculate the excitations of the short-, middle-, and long-wave cones, we used the Stockman–Sharpe 10° fundamentals (2000), which are appropriate for our extra-foveal targets. We represent our stimuli in a chromaticity diagram (Fig. 2) designed to be analogous to the diagram that MacLeod and Boynton (1979) constructed from the 2° fundamentals of Smith and Pokorny (1975). To retain as far as possible the familiar structure of the MacLeod–Boynton diagram, we have scaled the Stockman–Sharpe 10° fundamentals to have the same relative heights as the Smith–Pokorny 2° fundamentals; and we have scaled S to give a value of 1.0 at the maximal value of $S/(L + M)$, as in the classical diagram. As an analogue of Judd (1951) luminance, we took the sum of the scaled long-wave and middle-wave signals $(L + M)$. Our referent stimuli were adjusted to have the same value of $(L + M)$ as the white background, which had a CIE (1931) luminance of approximately $10 \, \text{cd} \, \text{m}^{-2}$ and a CIE (1931) chromaticity of $x = 0.328$, $y = 0.322$. Our test stimuli had the same average value of $(L + M)$ as the background and the referent patches, but the value on any one presentation was jittered randomly in the range $\pm 5\%$, to prevent the use of luminance cues to solve the task. It is very unlikely that our thresholds were affected by rod intrusion, since the Weber fractions measured were very much smaller than those classically found for rod vision (Wyszecki & Stiles, 1967, Table 7.4).
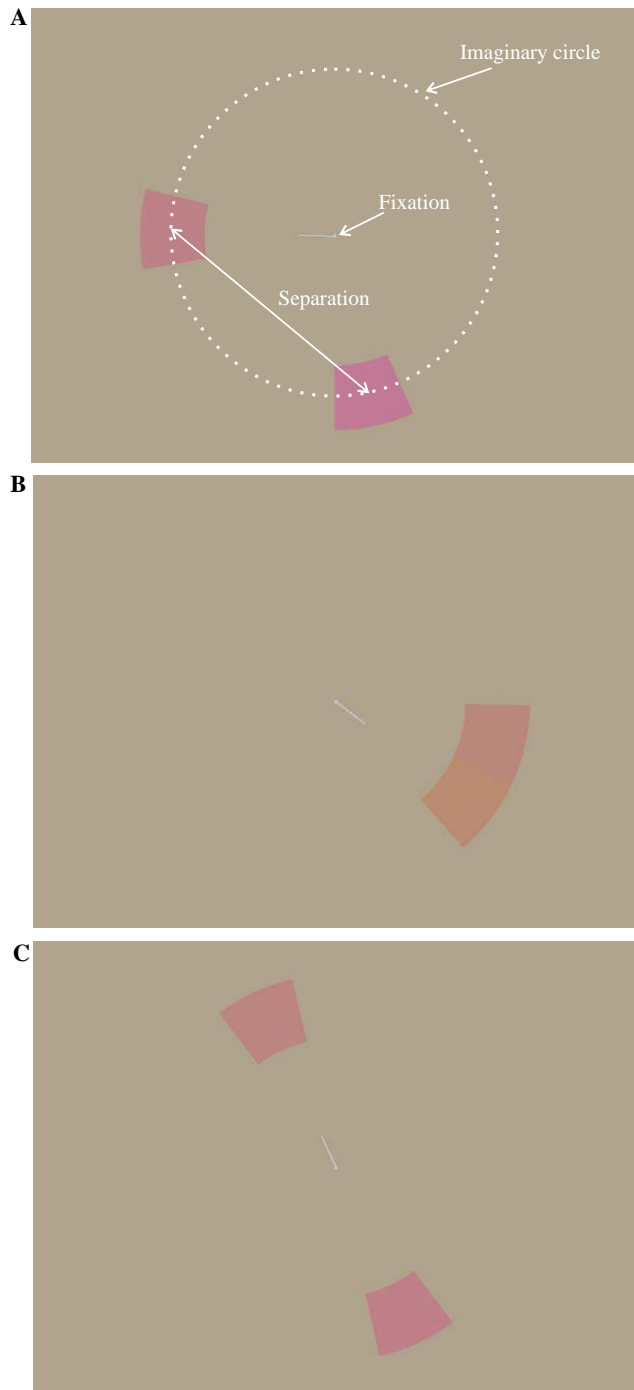
A

B

C

Fig. 1. Illustrations of the stimuli used in the experiments. The target patches were sectors of an annular ring centred on the fixation point. The centres of the patches lay on an imaginary circle of diameter 5° of visual angle (A). Separation is expressed as the linear distance between the centre points of the patches. (B) A case where the patches are at their minimum separation (2° of visual angle), while (C) shows a case where they are their maximum separation (10°). An achromatic background was always present.
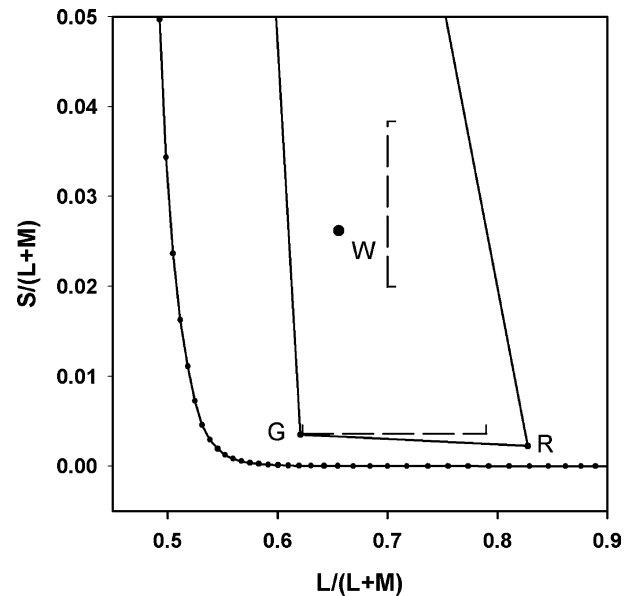

Fig. 2. The ranges of stimuli used in Experiment 1, represented in an analog of the MacLeod–Boynton 2° chromaticity diagram. The present diagram is constructed from the 10° fundamentals of Stockman and Sharpe (2000). The ordinate of the diagram represents the excitation of the short-wave cones relative to the sum of the long- and middle-wave cone excitations, while the abscissa represents the relative excitation of the long- and middle-wave cones. These axes are thought to correspond to the signals of the two chromatic channels found in the early visual system (Derrington et al., 1984). In the present experiments, stimuli were chosen to differ along only one or the other of the two axes. The ranges used in Experiment 1 are shown by the broken lines. The point marked W in the diagram corresponds to the white background that was continuously present. R and G represent the chromaticities of the red and green phosphors of our monitor, and the solid lines delimit the gamut available on the monitor.

2.3. Instrumental variation

If we wish to measure the variation in discrimination with increasing separation, we need to know the instrumental variation in chromaticity between different points on the screen, since physical differences might be larger the more remote the points on the screen that are compared. We spent some time identifying regions of our Sony screens that exhibited minimum variation. We measured the chromaticity of sample targets at positions on our imaginary circle at 45° intervals from 12 o'clock (0°). For the selected region of the St. Petersburg monitor, the maximal difference in $L/(L + M)$ was 0.1%, between positions 0° and 135°, and in $S/(L + M)$ was 1.6% between positions 0° and 315°. For the Cambridge monitor, the corresponding values were 0.2% between 180° and 270° and for $S/(L + M)$ was 1.2% between 45° and 180°. All other differences were smaller than these limiting values.

2.4. Procedure

We estimated thresholds along the two cardinal axes of colour space (Krauskopf et al., 1982), which correspond to the two axes of the modified MacLeod–Boynton diagram (Fig. 2): in one case, the short-wave cone (S) signal was held constant and only the ratio of the long-wave and middle-wave cone signals was varied; and in the other case, the S signal was varied and the L/M ratio was held constant. When discrimination along the L/M axis was tested, the

S value was 0.0036, a value less than the *S* value of the white background, and when the *S* axis was tested, the *L* value was 0.7, a value greater than the *L* value of the white background. Our reason for adopting these offsets, and not simply measuring departures in two directions from the white background, was that we wished explicitly to measure hue discrimination and not saturation discrimination.

Thresholds were measured by a method of two-alternative spatial forced choice. Within a single block of trials, the separation of the stimulus patches was held constant. When the *L/M* axis was being tested, the subject's task was to indicate by pushbuttons whether the more clockwise of the two stimuli was the redder or the greener. When the *S* axis was tested, the subject indicated whether the more clockwise stimulus was bluer or less blue. On any trial, one stimulus was conceptually the reference stimulus and the other was the variable stimulus, but the subject could not predict which of the two would be in the more clockwise position. Tone signals indicated to the subject whether his response was correct or incorrect.

The difference between the test and referent stimuli was adjusted according to an adaptive staircase rule: after three correct responses, the difference was reduced and after an incorrect response, it was increased. This three-to-one rule converges to 79.4% correct responses (Wetherill & Levitt, 1965). The step size was 10% of the difference between test and referent. Data from the first five reversals of the staircase were not used, and the subsequent 10 reversals were averaged to give an estimate of the threshold.

2.5. Subjects

The subjects comprised one male (JM) and four females (MD, IK, KM, and ED). All were shown to have normal colour vision by the Cambridge Colour Test (Regan, Reffin, & Mollon, 1994). Subjects IK, KM, and ED were naïve as to the purpose of the experiments.

3. Experiment 1: Preliminary measurements

In earlier measurements on the discrimination of spatial variables (Danilova & Mollon, 2003), in order to establish that the subject actively compared two stimuli, we developed a method in which the referent stimulus is varied from trial to trial but the ratio of the variable stimulus to the referent is adjusted according a single staircase. This requires us to identify a range of the stimulus variable over which the Weber fraction is close to constant. For each subject, we therefore made preliminary measurements to establish a suitable range on each of the cardinal axes of colour space.

3.1. Procedure

Separate series of measurements were made for the two cardinal axes (see Section 2). For the *L/M* axis, we held *S* constant at a value of 0.0036 and chose a range of 10 referent chromaticities that spanned the *L/M* value of the white background. In Fig. 2, the range of these green, yellow, and orange referents is shown as the horizontal broken line. For the *S* axis, we similarly chose a range of 10 chromaticities that held constant the *L* value at 0.7 and spanned the *S* value of the white background. In Fig. 2, the range of these orange, salmon, and purple referents is shown as the vertical broken line.

Within one experimental session, the 10 referent stimuli were randomly mixed but separate staircases were maintained for each referent. Within one session, the spatial separation of the stimulus patches was held constant. Separation was varied between sessions, and each subject completed at least five sessions for each separation tested.

3.2. Results

Examples of our preliminary measurements are shown in Fig. 3. The upper panels give data for the case where the variation is on the *L/M* axis, and the lower panels for the case of variation on the *S* axis. Thresholds are shown as a function of the size of the *L* signal or the *S* signal of the referent patch. The corresponding value of the steady white background is indicated as a vertical arrow. The parameter in each panel is the spatial separation of the referent and test patches.

Discrimination is optimum when the referent signal is close to the background value for a given axis. This is the result classically found if the adaptation of the eye is held constant, and discrimination is probed at chromaticities that lie at various distances from the background value (Krauskopf & Gegenfurtner, 1992).

Three additional features of these preliminary measurements are of note:

(i) The lowest thresholds are typically obtained when the centres of the stimulus patches are separated by 3.14° of visual angle, i.e., when there is gap of approximately 1° between them.
(ii) The effect of spatial separation is greatest when the referent *L* signal or *S* signal is most distant in chromaticity from the value of the background.
(iii) On the *L/M* axis, for all separations, the referent colour that gives optimum discrimination is an intermediate shade of yellow green rather than a pure yellow.

The third finding allows us to eliminate one hypothesis that we considered when we were designing this experiment. We supposed that the locus of optimum discrimination might shift along the *L/M* axis as spatial separation increased: at small separations, the thresholds might be lowest when the referent and the background were tritan metamers (i.e., when the *L* value of the referent coincided with the *L* value of the field to which the eye was adapted), but at large separations the optimum might re-centre itself on the chromaticity of unique yellow (in Fig. 2 the locus of lights that are neither reddish nor greenish runs obliquely from the white point to a point near 0.7 on the abscissa).
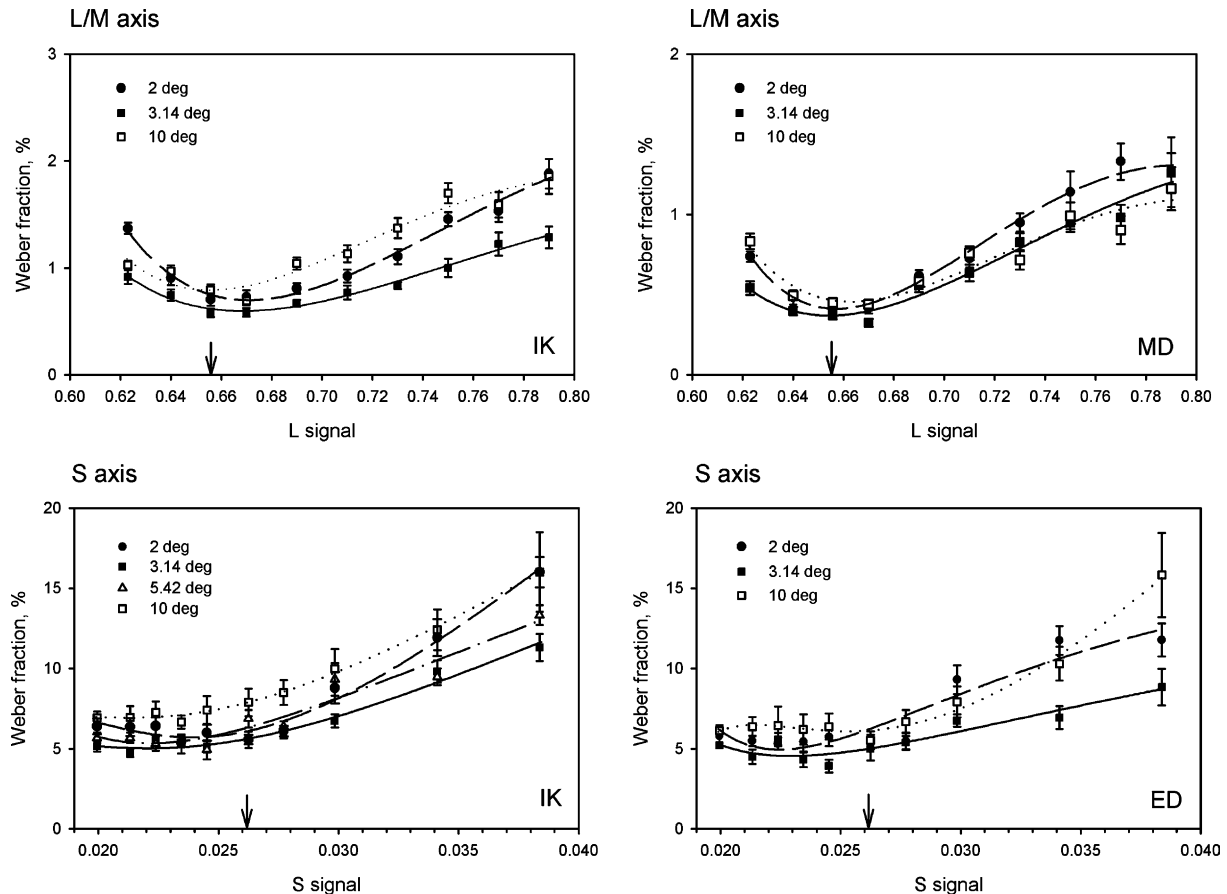
Fig. 3. Chromatic discrimination at different positions along the *L/M* axis (upper panels) and *S* axis (lower panels). The arrows indicate the value on the abscissa corresponding to the steady white background to which the observer was adapted. The parameter in each panel is the spatial separation (in degrees of visual angle) of the centre points of the two stimulus patches. Error bars: ±1 SEM. The smooth curves fitted to the data points are inverse third-order polynomials and are not intended to have theoretical significance.

This outcome could be predicted if the discrimination of distant patches depended on the comparison of central, categorical representations. Opposite departures from unique yellow might be more efficiently encoded than different shades of yellow-green. In the event, there is no support in our data for a hypothesis of this kind.

4. Discrimination as a function of separation

From the preliminary measurements, we identified stimulus ranges where the threshold was approximately constant for a given subject. These were the ranges used in Experiment 2. For the *L/M* axis, the chosen range was the shallow minimum of the function. These stimuli comprised green, yellow, and orange colours with chromaticity coordinates $S/(L + M) = 0.0017$ and $L/(L + M) = 0.649–0.681$ (IK), 0.641–0.689 (JM), 0.641–0.667 (KM), 0.640–0.680 (MD). For the *S* axis, the chosen range corresponded to a region largely lying below the background value of *S*. These stimuli comprised salmon, pink, and purple colours with chromaticity coordinates $L/(L + M) = 0.7$ and $S/(L + M) = 0.0201–0.0247$ (IK), 0.0204–0.0276 (JM), 0.0204–0.0276 (ED), and 0.0211–0.0258 (MD).

4.1. Procedures

In order to ensure that the subject actively compared the two stimulus patches (see Section 1.3), the chromaticity of the reference stimulus took on a random value from 25 values equally spaced across the selected range. There were not separate staircases for each of the 25 possible reference stimuli. Rather, what was adjusted from trial to trial was a ratio of chromaticities, the percentage difference in the *L* (or the *S*) value between the test and referent stimulus.

In each experimental session, nine different separations were tested in different, randomly ordered, blocks of trials. There was also a tenth condition in which only a single stimulus patch was presented. When the *L/M* axis was being tested, the subject was asked to indicate whether this single patch was greener or redder than the average of all the stimuli presented in the experiment. When the *S* axis was tested, the subject was asked whether the single patch was 'more or less blue' than the average of all the stimuli presented. In this 'absolute judgement' condition, 21 different stimuli were used, covering all but the extremes of the range of referents used in the other nine conditions. Each

stimulus was presented four times, in randomised order. The 'absolute judgement' condition was randomly placed within a session with the restriction that it could not be the first block.

Each subject completed at least 14 sessions, each of 10 blocks.

4.2. Results

Our primary results are given in Fig. 4 and show how chromatic discrimination varies with the spatial separation of the discriminanda. Fig. 4A shows thresholds on the *L/M* axis for individual subjects. Thresholds are given as the percentage change in the *L* signal that is needed to sustain 79% correct performance. Since the absolute values of the threshold vary between subjects, a logarithmic ordinate is used. The error bars correspond to ±1 standard error of the mean. Fig. 4B shows the average data for the four subjects. In order to give equal weighting to subjects with different absolute levels of performance, the thresholds were

expressed as a ratio of the threshold at minimum separation, i.e., the threshold when the stimulus patches are abutting.

For all subjects, discrimination appears to be optimal not when the two stimulus patches are abutting but when there is a small separation between them, i.e., when the centre-to-centre separation is approximately 3° and there is a gap of 1°–2° between the patches. At greater separations, the threshold rises. A repeated-measures ANOVA shows that the effect of separation is highly significant ($F_8 = 5.5$, $p < 0.001$). Post hoc contrasts with Bonferroni correction show that the third separation (3.14° between midpoints) differs significantly from separations 6, 7, 8, and 9 ($p = 0.024$, $p = 0.027$, $p < 0.001$, and $p = 0.004$, respectively).

Fig. 4C shows thresholds on the *S* axis for individual subjects. The absolute values of the thresholds on this axis are higher than on the *L/M* axis, as is classically found (Cavonius & Estévez, 1975; Wyszecki & Stiles, 1967, p. 577). Thresholds are given as the percentage change in the *S* signal that is needed to sustain 79% correct performance.
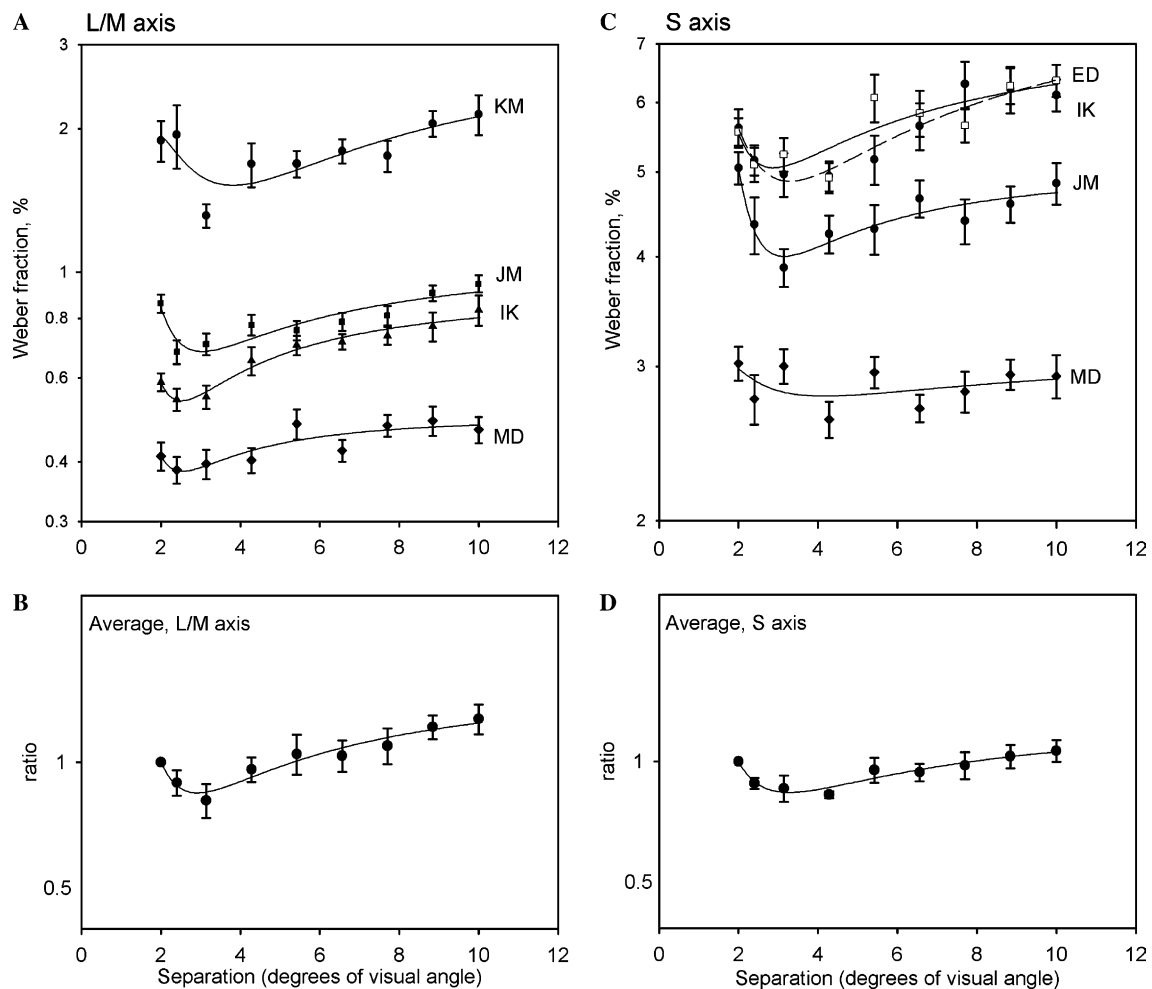

Fig. 4. Chromatic discrimination as a function of spatial separation. (A) Thresholds for the *L/M* axis for four subjects, while (C) shows thresholds for the *S* axis. In order to accommodate subjects with different absolute levels of performance, a logarithmic scale has been used for the ordinates of these panels. Error bars: ±1 SEM. (B and D) Corresponding averages. To give equal weighting to each subject, we expressed each subject's threshold as a ratio of his or her threshold at minimum separation. It is the average of these ratios that is plotted. The smooth curves fitted to the data points are inverse third-order polynomials and are not intended to have theoretical significance.

We again use a logarithmic ordinate to accommodate variations between subjects. Fig. 4D shows the average data for the S axis for the four subjects, expressed as a ratio of the Weber fraction at the minimum separation.

Except in the case of MD, whose function is almost flat, the data for the S axis resemble those for the L/M axis: discrimination is optimum not when the patches are abutting but at an intermediate separation. Thresholds then rise as separation is increased. A repeated-measures ANOVA shows a highly significant effect of separation ($F_8 = 6.1$, $p < 0.001$). Post hoc contrasts with Bonferroni correction show that the third and fourth separations (3.14° and 4.3° between midpoints) differ significantly from the smallest separation ($p = 0.003$, $p = 0.013$) and from the largest ($p = 0.036$, $p = 0.006$). The fourth separation also differs significantly from separations 6, 7, and 8 ($p = 0.036$, $p = 0.036$, $p = 0.023$).

4.2.1. Hemifield differences

4.2.1.1. Left versus right; Upper versus lower. A neuropsychological tradition holds that the right hemisphere has a disproportionate role in colour discrimination: impairments of colour discrimination are reported more frequently after right-sided than after left-sided, unilateral, lesions (De Renzi & Spinnler, 1967; Scotti & Spinnler, 1970); and a left-field superiority has been described when normal subjects are required to discriminate Munsell chips exposed tachistoscopically to the left or right of fixation (Davidoff, 1976; Hannay, 1979). It is useful to ask whether a left hemifield superiority is present in our own data, since our task is one that encourages subjects to distribute attention uniformly across the visual field and is one that requires discrimination at the limits of performance.

On each trial, our experimental program centres the pair of discriminanda randomly on an imaginary circle concentric with the fixation point. A single staircase adjusts the chromatic difference between the paired stimuli, independently of the position chosen on a single trial. Thus, our primary program does not separately estimate thresholds for different regions of the visual field. Nevertheless, the program visits different positions even-handedly and so we can retrospectively recover from our data the totals of correct and incorrect judgements for particular regions of the imaginary circle (thus checking our own assumption that discrimination is approximately similar at all points on the circle). We have compared left versus right hemifields, and also upper versus lower hemifields. For each subject and for each axis of colour space, we derived the percent correct trials separately for all separations used, excluding only the largest separation (10°), where the discriminanda necessarily fall in different hemifields. In the case of the remaining separations, we included all those trials where both stimuli fell within one hemifield. We collapsed data across separations and then performed two-tailed 2×2 χ^2 tests to estimate whether there was a significant difference in correct responses between hemifields.

The results of these analyses are shown in the histograms of Fig. 5. For the L/M axis of discrimination, subjects MD, JM, and KM showed no significant difference between left and right hemifields. One subject, IK, showed a significant difference, but opposite to that expected from the earlier literature, in that she had higher scores in the right visual field ($\chi^2 = 14.07$, df $= 1$, $p < 0.001$). The absolute difference in her scores was small: 81.5% correct versus 85.5%. For the S axis of discrimination, subjects MD and IK showed no significant difference, JM showed a marginally significant advantage for the left visual field ($\chi^2 = 4.90$, df $= 1$, $p < 0.05$) whereas ED showed a significant advantage for the right field ($\chi^2 = 8.05$, df $= 1$, $p < 0.01$).

A comparison of upper and lower hemifields revealed that only MD showed a significant difference: for both axes, her scores are higher in the lower field ($\chi^2 = 5.45$, df $= 1$, $p < 0.02$ for L/M axis; $\chi^2 = 17.44$, df $= 1$, $p < 0.001$ for S axis). The absolute sizes of the percentage differences are not large (see Fig. 5, middle panels); and none of the remaining subjects showed a significant difference on either axis.

In sum, we found no consistent hemifield effects. Where significant effects were found, they were relatively small in percentage terms; and only one subject for one chromatic axis showed the left-field advantage that might be expected from the neuropsychological literature. The absence of a systematic left-right difference in chromaticity discrimination is consistent with the results of Baumgardt and Chiron (1965) who found no left-right difference in luminance discrimination at the same eccentricity that we used here.

4.2.1.2. Is discrimination impaired when the comparison is between hemispheres? A particularly interesting comparison is that between trials on which both targets fell within either the right or the left hemifield and trials on which the targets fell in opposite hemifields. In the latter case, any cortical comparison requires that information should be transmitted across the corpus callosum. Does this lead to a degradation in the representation of the stimulus and thus to a poorer performance?

For this analysis, since thresholds do vary with separation (Fig. 4) and since stimuli at small separations are more likely to fall within one hemifield, we considered only the case where the stimulus separation was 7.6°. In this condition there are very nearly the same number of trials in which both stimuli occur within one hemifield and in which the two stimuli fall in opposite hemifields. We calculated the total correct and total incorrect trials for the same-hemisphere and different-hemisphere conditions. We used a two-tailed 2×2 χ^2 test to ask whether there were significant differences between conditions.

The results of this analysis are shown in the rightmost panels of Fig. 5. No subject showed a significant difference between the same- and different-hemisphere conditions. This was true for both axes of colour space. Thus, we have no evidence for an additional degradation of performance in conditions where the comparison requires obligatory transmission between hemispheres.
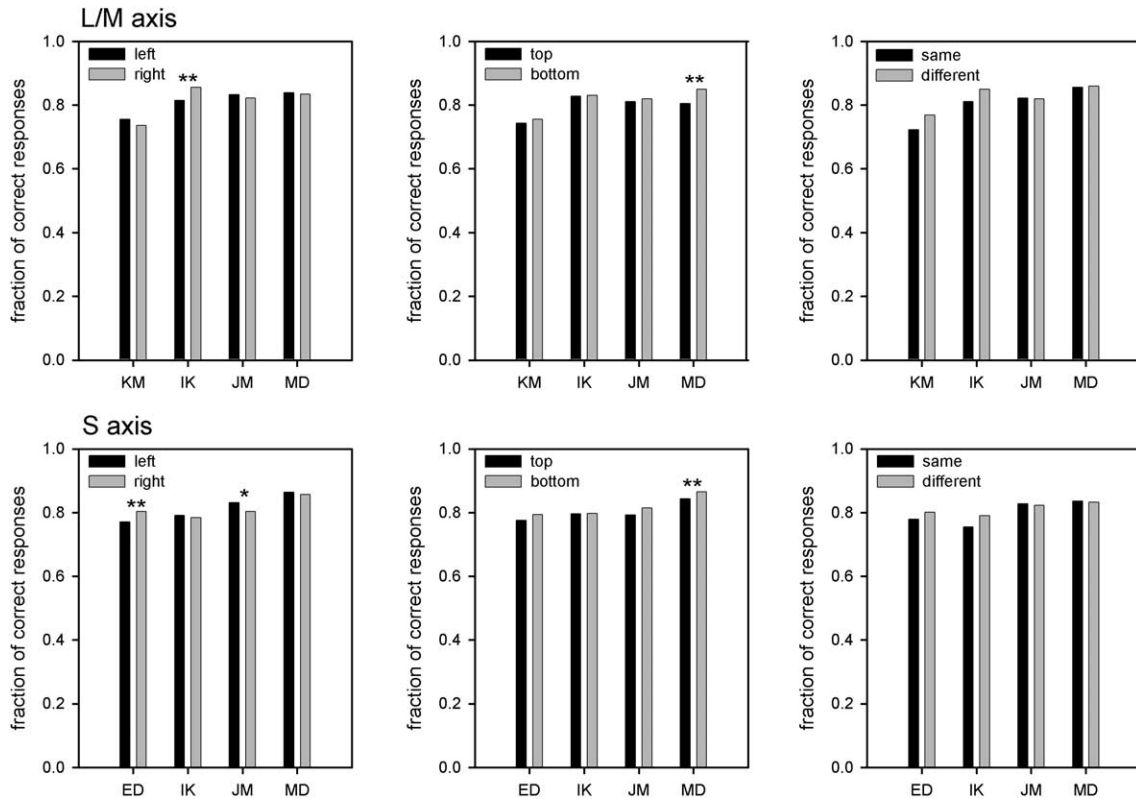
Fig. 5. Histograms showing comparisons of performance for different subsets of trials. The leftmost panels show comparisons of left and right visual fields for each subject, while the central panels show comparisons of upper and lower hemifields. The rightmost panels compare trials on which both stimuli fell in the same hemifield (left or right) and trials on which they fell in opposite hemifields. The upper panels show data for the *L/M* axis and the lower panels for the *S* axis. Asterisks indicate the small number of conditions where a significant difference was present. Note that the average level of performance in these panels does not correspond exactly to 79% correct: this is because in this analysis we included all trials on a given staircase, not just those encompassed by the last 10 reversals of the staircase.

4.2.2. Absolute judgements

In each experimental session, we included a condition in which the subject was required to make an absolute judgement as to whether a single stimulus patch was above or below the mean of all stimuli presented in the experimental run. Characteristic data are shown in Fig. 6: in the upper panels, the probability of the report 'redder' is plotted as a function of the *L* value of the single stimulus, and in the lower panels, the probability of the report 'bluer' as a function of the *S* signal. To compare the precision of these absolute judgements with the difference thresholds measured in the other conditions, we fitted each set of data with a sigmoid function and took as measure of precision the change in the *L* or in the *S* signal needed to alter the reports from 50% 'redder' or 50% 'bluer' to 79.4%. For the *L/M* axis, the estimated values were 0.78%, 1.37%, 0.81%, and 0.70% for subjects IK, KM, JM, and MD, respectively. For the *S* axis, the values were 3.85%, 6.20%, 4.46%, and 2.73% for subjects IK, ED, JM, and MD, respectively. Subjects sometimes show constant errors, in that the 50% points do not correspond exactly with the midpoints of the stimuli presented in the absolute judgement condition (indicated by vertical arrows in Fig. 6).

Our subjects make absolute judgements with a precision that is comparable to their thresholds in the discrimination conditions. This finding illustrates the need to ensure, in all discrimination experiments, that subjects actively compare the two external discriminanda and do not simply compare a single target to an internal template. To ensure that our subjects in our main experiment did compare the two targets, we used not a single reference stimulus but 25 closely spaced referents. Moreover, the subject could not predict whether the referent or the variable stimulus would be the more clockwise on a given trial. For our best subjects, the measured thresholds were 6–12 times smaller than the range of referents. It is very unlikely that our subjects could achieve this performance by basing their judgement on just one of the two stimuli, say, the more clockwise patch. Nevertheless, we made an empirical test, described in the next section.

4.3. Control measurements

In a control experiment, we compared two conditions. In Condition A, the stimuli and procedures were as in the main conditions of the preceding experiment (Section 4.1), and the subject was asked to make discriminations as before—between a test patch and a referent patch that could take on any of 25 finely spaced chromaticities. In Condition B, the computer program was exactly the same except that the less clockwise stimulus was suppressed on every trial. In this case,
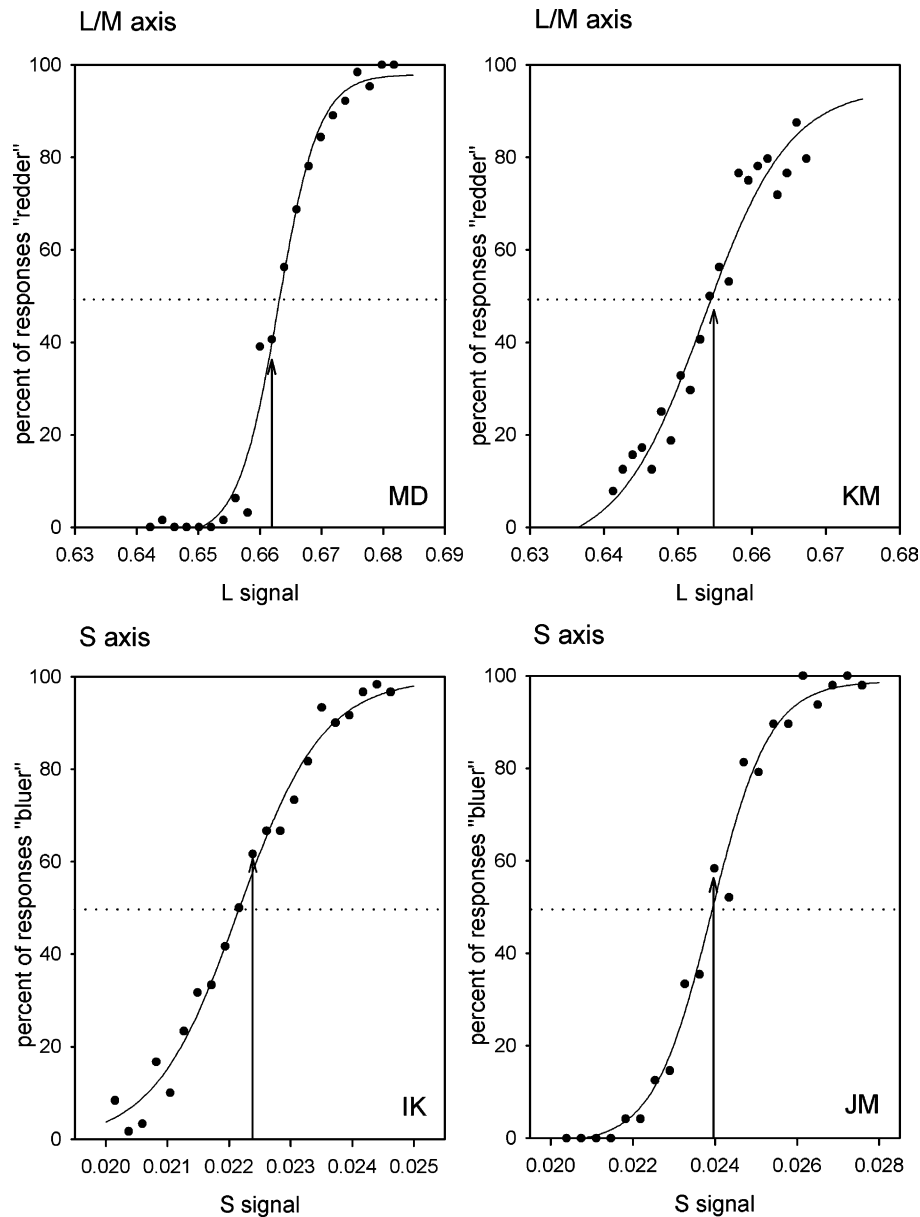
Fig. 6. Examples of psychometric functions for absolute judgements. These data were obtained in an additional condition interleaved with the other conditions of the main experiment. Subjects were asked to categorize the target colour relative to the average of all stimuli presented in the experiment. The graph shows the probability of responding 'redder' (*L/M* axis) or 'bluer' (*S* axis) as a function of the *L* or the *S* signal. The vertical arrows show the objective average stimulus, and the horizontal broken line represents the level at which the alternative responses are equally frequent. The horizontal distance between the arrow and the 50% point on the psychometric function represents the constant error or *accuracy* of the judgements, whereas the slope of the psychometric function represents the *precision* of the judgements.

the subject was asked to base a decision on the single stimulus presented, *as if the second had been present*. A single separation of 5.8° of visual angle was tested. The *L/M* and S axes were tested in different experimental series. For each axis and for each of the two conditions, subjects completed at least 20 independent blocks of trials. A single experimental sessions consisted of five repetitions of Conditions A and B, randomly interleaved, with the restriction that Condition B was never the first condition in a session.

The results of the control experiment are shown in Fig. 7, where the black bars correspond to Condition A and the grey bars to Condition B. The error bars correspond to

±1 SEM. For the standard Condition A, our subjects (with the one exception of KM for the *L/M* axis) achieve thresholds similar to those obtained at this separation in the main experiment (Fig. 4), but when an external comparison stimulus is not available (Condition B), thresholds are much greater for all subjects and all axes. This result confirms that the jitter imposed on our referents, and the randomisation of the position of the test patch, do ensure that the subject actively compares the two discriminanda. If it were the case that the subject attended to only one of the two stimuli on a given trial, there should be no difference between his performance in the two conditions.
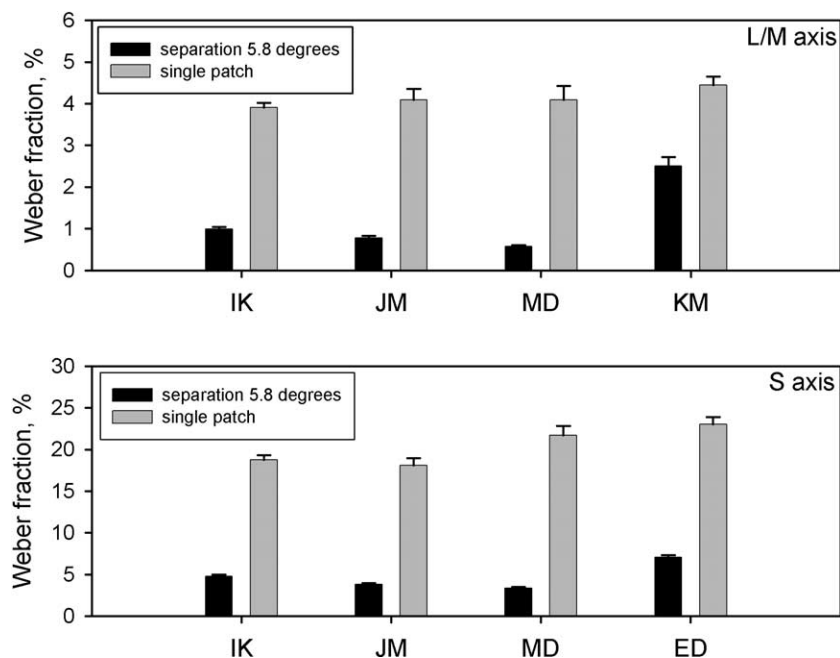
Fig. 7. Results of a control experiment to determine the level of performance that subjects can achieve if one of the two targets is suppressed. The black bars show the thresholds when two targets are presented at a separation of 5.8°. The grey bars show thresholds when only the more clockwise of the two stimuli is actually presented to the subject. Error bars: ±1 SEM.

5. Discussion

Our chief finding is shown in the lower panels of Fig. 4. At a constant eccentricity of 5°, chromatic discrimination depends on the spatial separation of the discriminanda, but performance is not optimal when the stimulus patches are juxtaposed. Rather the threshold first falls as a small separation is introduced and then rises as separation increases up to 10° of visual angle. This behaviour is seen for both the *L/M* and the *S* axes of colour space: the average functions are similar for the two axes.

5.1. The gap effect

The initial fall in threshold at small separations recalls the 'gap effect' described by Boynton et al. (1977) for bipartite foveal fields. Boynton and his colleagues found that a small gap improved discrimination along a tritan axis (i.e., when only the *S* signal is varying), whereas discrimination of luminance was impaired by a gap. Discrimination on an *L/M* axis was little changed. Even for the tritan axis, the foveal gap effect was not found when a forced-choice method was used. This was confirmed by Eskew (1989), although Montag (1997) did obtain an attenuated gap effect with forced choice. Eskew reported also that the foveal gap effect was reduced at short exposures (400 ms). For parafoveal stimuli, our results exhibit a gap effect for both axes of colour space, for forced-choice conditions and for short (100 ms) exposures. It appears that the gap effect may be more robust at an eccentricity of 5° of visual angle, the eccentricity used in the present experiments. A classical

explanation of the foveal gap effect is that chromatic signals are integrated over a significant area and that a gap or contour between the stimulus fields serves (by an unknown mechanism) to delimit the regions of integration. It is very reasonable to suppose that integration areas for chromatic signals are larger in the periphery. An analogy might be made with the second-stage integration of features that is thought to underlie the peripheral crowding effect for spatial features (Levi, Hariharan, & Klein, 2002; Parkes, Lund, Angelucci, Solomon, & Morgan, 2001; Pelli, Palomares, & Majaj, 2004).

5.2. Comparison of colour discrimination with the discrimination of spatial attributes

For our stimuli at 5° eccentricity, we find that colour discrimination is optimal when the centres of the stimuli are separated by 3°–4° of visual angle and thus when there is a gap of 1°–2° between their closest edges. As separation is increased further, discrimination slowly deteriorates; and when the targets are 10° apart, thresholds for the *L/M* axis are 60% greater than at the optimal separation (Fig. 4B). For the *S* axis, the corresponding difference is of the order of 30% (Fig. 4D). This increase of thresholds with spatial separation resembles the result we have previously obtained for two practised subjects when discriminating the orientation of Gabor patches (Danilova & Mollon, 2003; Fig. 8, panels a and c), but differs from the case of spatial frequency, where we have found essentially no change of threshold as separation in the visual field is varied.

5.3. The mechanism of comparison

At separations where discrimination is optimum—when the edges of the targets are separated by approximately 1°—it would be possible to suppose that discrimination depends on a difference signal provided by dedicated second-order comparators that compare the chromaticities of nearby retinal regions. And such comparators could be identified with the double-opponent cells that have been described in the visual cortex (Michael, 1978a). The difference signal supplied by such hard-wired comparators would be analogous to the difference signal provided by cells sensitive to local contrast of luminance (see Section 1.1).

However, even at a separation of 10° and even when the two stimuli fall in opposite hemifields (Fig. 5), performance is still remarkably good: for chromatic discriminations on the L/M axis, the absolute values of the thresholds range from approximately 0.4% to 2% (Fig. 4A), while for the S axis, they range from approximately 3% to 6% (Fig. 4C). Even though some decline of performance does occur as separation increases, we still need an explanation of the subject's ability to make fine comparisons of brief, peripheral stimuli that are presented many degrees apart. The mechanism of such comparisons has seldom been discussed.

We could suppose that over the whole range of separation, the comparison is achieved by dedicated comparator neurons. It is always possible to postulate a higher-order cell that draws signals of one sign—excitatory or inhibitory—from low-level, colour-specific cells whose receptive fields coincide with one of the two target patches, and a signal of the opposite kind from cells whose receptive fields coincide with the second patch. The difficulty with such models is the combinatorial explosion of second-order cells—the large number of dedicated comparators required if the observer is to be able to compare, at the experimenter's whim, any two specific points in the visual field (Danilova & Mollon, 2003, pp. 410–411). Not only is there a multiplication in the number of neurons, but perhaps more significantly there is a vast increase in white matter, corresponding to the many dedicated axons required to bring together the signals from pairs of lower-order cells that are remote from one another.

The question of whether chromatic discrimination is carried out by dedicated comparator units is only a small part of a larger, and quite unsolved, question. That is the question of whether—at a central level in the brain—attributes, objects, and concepts are represented by the activity of single neurons (Barlow, 1972). A major problem with such a theory is this: if an entity or an attribute can be represented in the brain only by the activity of a gnostic unit, then the only way to make that information available to other stations in the brain is to cast a dedicated axon between the two points. This would be like constructing the Internet by running a cable between any two nodes that needed to communicate. It does appear inescapable that single neurons represent particular features or stimuli in peripheral sensory systems. However, we have suggested elsewhere that central representations are of a different kind and that the brain must have some—yet unknown—code that can be transmitted by a cerebral bus independently of the neurons carrying the code (Danilova & Mollon, 1999, 2003).

The question that we raise has a developmental or adaptational aspect to it: how is a uniform calibration established across an inhomogeneous visual field, so as to allow the subject to make precise comparisons of attributes such as hue, spatial frequency and contrast at large separations? Presumably, the calibration that underlies our 'spatial constancy' is carried out during movements of the eyes across a field of objects or while we ourselves manipulate an object and displace its position on our retina.

5.4. The mechanism of lateral interaction may be distinct from the mechanism of comparison

The increase in chromatic threshold with separation (Fig. 4) might nevertheless be taken as evidence for some form of lateral interaction that changes with distance. Such lateral interaction may improve discrimination and yet need not be one and the same as the mechanism of comparison. It is known that axons extending laterally for as much as 6-8 mm are present in the visual cortex of the cat (Alexeenko, Toporova, & Makarov, 1999; Gilbert & Wiesel, 1989), while values for macaque range from 2.1 mm for V1 to 5.7 mm for V4 (Amir, Harel, & Malach, 1993). In macaque V1, in a region equivalent to an eccentricity of 5°, a cortical distance of 2 mm would be very roughly equivalent to 3° of visual angle at constant eccentricity (Van Essen, Newsome, & Maunsell, 1984). One of the roles of such lateral connections may be to provide contextual information for the purpose of maintaining colour constancy (Land, 1974). And a by-product of this interaction may be an enhanced differentiation of colour signals from nearby regions of the visual field—perhaps by a process of lateral inhibition. Nevertheless, the actual *comparison* of these signals may be carried out more centrally—and not necessarily by hard-wired neural comparators.

5.5. The role of the achromatic field

In a preliminary experiment, we tried presenting our brief (100 ms) stimulus patches against a dark field. Under these conditions, chromatic discrimination is poor. And the conditions are ones that would rather seldom occur in the natural world. We therefore presented our stimuli against a steady achromatic field of luminance similar to that of the targets. Whittle (2003) has argued persuasively that colour perception depends on cone contrast signals, that is, on the differences between cone signals deriving from the background and signals deriving from the target. And certainly the achromatic background has a critical role in our experiments. We found—as has been found previously (e.g., Krauskopf & Gegenfurtner, 1992; Miyahara, Smith, & Pokorny, 1993; Schönfelder, 1933)—that discrimination

was optimal when the chromaticity of the surround and that of the target were similar: for discriminations on the tritan axis, thresholds were lowest when the field and target had similar S values, and for discriminations on the L/M axis, thresholds were lowest when field and target had similar L values (Section 3.2 and Fig. 3). But is it the temporal or the spatial contrast with the field that is critical? This is one of the outstanding issues in colour science (see Section 1.1). When an observer compares two stimuli that lie 10° apart in the visual field, he may be comparing signals that derive from the body of the stimulus patch, signals that are scaled by the adaptive state of the cones at the moment of onset of the patch; or he may be comparing spatial difference signals that derive from the edge between the coloured patch and the achromatic background. In the latter case, the local contrast signals may be extracted by double-opponent neurons. This hypothesis, however, is distinct from the suggestion that double-opponent neurons subserve the comparison of well-separated patches. It is the latter proposal that we question.

Acknowledgments

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