The symmetry of visual fields in chromatic discrimination

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ABSTRACT

Both classical and recent reports suggest a right-hemisphere superiority for color discrimination. Testing highly-trained normal subjects and taking care to eliminate asymmetries from the testing situation, we found no significant differences between left and right hemifields or between upper and lower hemifields. This was the case for both of the cardinal axes of color space. In addition, there was no difference according to whether the discriminanda were delivered to the same or to different hemispheres, and we note that the same number of synapses may lie between the retina and the site of comparison whether or not the stimuli are delivered to the same hemisphere.

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1. Introduction

1.1. Evidence for hemispheric asymmetry in color perception

Does the right cerebral hemisphere have a disproportionate role in the perception of color? A positive answer is suggested by two classical sources of evidence: studies of patients with unilateral lesions and studies of hemifield differences in normal subjects.

Although a unilateral lesion never leads to a complete and permanent achromatopsia (Meadows, 1974), two statistical studies of patients with unilateral lesions suggested that impairments of chromatic discrimination were more frequent after right-sided lesions than after left-sided. De Renzi and Spinnler (1967) tested 173 patients and 100 controls on the Ishihara plates and on a task in which the subject was required to identify the matching pairs in two identical sets of colored papers. On both these tests, a greater percentage of patients in the right-sided group fell below criterion performance compared to the left-sided group. Scotti and Spinnler (1970) tested 168 unilateral patients and 80 controls on the Farnsworth-Munsell 100-hue test, a test that requires very fine discrimination for perfect performance. Error scores were significantly higher for patients with right-sided lesions than for those with left-sided lesions, and this effect was traceable to the subgroup of right-hemisphere patients who had a visual field defect. Left hemisphere patients with field defects were not similarly impaired

and so Scotti and Spinnler concluded that the result for right-hemisphere patients indicated not an effect of the field defect itself but of a right-sided post-rolandic lesion. This association with posterior lesions also perhaps rules out one traditional problem with statistical studies of the effects of left- and right-sided lesions—the problem that right-sided lesions may on average be larger because surgeons are more conservative in removing tissue from the speech-dominant hemisphere—although it does not rule out the problem (Young, 1983, p. 13) that the Farnsworth-Munsell is an intrinsically spatial task. A third statistical study, that by Assal, Eisert, and Hécaen (1969), examined 155 patients using the Farnsworth D15 test and found no difference in the effects of left- and right-sided lesions, but it must be said that the tokens of the D15 are very coarsely spaced in chromaticity and are designed for detecting inherited dichromacy.

In the case of normal subjects, left–right asymmetries have been reported for many sensory and perceptual functions. Where a superiority has been found for one or the other hemifield, this has been taken to suggest that the contralateral hemisphere is superior for that function (Kimura, 1966). It is supposed either (i) that the apparatus of analysis is unilaterally located and that material arriving via the other hemisphere is degraded in its passage across the corpus callosum, or (ii) that the apparatus of analysis is bilaterally located but is intrinsically superior in one hemisphere (see e.g. Helige, 1993; Sergent, 1983). Davidoff (1976) reported a left-field advantage for the discrimination of hue, implying a right-hemisphere superiority. He presented pairs of Munsell chips tachistoscopically to the left or the right of fixation. On any trial, the chips could be identical or could differ in hue, lightness being

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held constant. The difference in color was either 2.5 or 5 steps in the Munsell system. In a separate experiment, Davidoff found that subjects were also more accurate for left-field stimuli when the discrimination was one of saturation, i.e. chroma in the Munsell system. In a similar study, Hannay (1979) used chips that were either identical in hue or differed by 2.5 Munsell units and she similarly found an advantage for the left visual field. Most recently, a right-hemisphere superiority has been reported for reaction times to the transition between an achromatic field and an equiluminant colored target (Sasaki, Morimoto, Nishio, & Matsuura, 2007).

Modern imaging studies throw only limited light on whether there is an asymmetry in the process of chromatic discrimination. Functional magnetic resonance imaging has identified a ventral occipital region ('hV4') thought to be the human analog of the macaque cortical region V4 (Liu & Wandell, 2005; McKeefry & Zeki, 1997; Wade, Brewer, Rieger, & Wandell, 2002). This region, which exhibits a topographical representation of the visual field, is bilaterally represented in most subjects, although in two out of twelve subjects, McKeefry and Zeki (1997) observed it only in the left hemisphere. One provocative asymmetry has been observed by Brewer, Liu, Wade, and Wandell (2005): a color-activated region anterior and lateral to hV4 was seen only in the right hemisphere of five out of five subjects.

The ventral occipital color-processing areas have most commonly been revealed by subtracting the signal obtained when a field is modulated in chromaticity from the signal obtained when the field is modulated only in luminance. The role of such areas in the process of discriminating colors is not yet clear: the neural site at which spatially separated patches are compared, and the mechanism of the comparison, remain quite unknown (Danilova & Mollon, 2006, see Section 4.2).

1.2. Differences between upper and lower fields

There are reports of a difference between upper and lower hemifields in color discrimination by normal subjects. Gordon, Shapley, Patel, Pastagia, and Truong (1997) presented brief stimuli that varied on a red-green axis centered on yellow and asked their subjects to classify the stimuli as reddish or greenish. A white masking stimulus followed the test stimulus. The precision of discrimination was estimated from the slope of the psychometric function and was found to be 2–3 times higher in the upper field than in the lower. Levine and McAnany (2005) presented target disks embedded in an array of distractor disks, which differed slightly in hue from the targets. The target disks were 12° above or below the fixation point and subjects were asked to report the spatial position of the targets relative to the vertical midline. Accuracy was significantly higher on trials in which the targets fell in the lower hemifield. Pennal (1977) required subjects to match a color presented in one quadrant to one of a circular array of 24 colored disks on a response box. Performance was poorest for the upper right quadrant of the visual field.

These functional differences between upper and lower fields might be explained by a difference between inferior and superior retina in the density of photoreceptors and ganglion cells (Curcio & Allen, 1990); but there may also be differences at a cortical level, such as that postulated to explain the finer resolution of attentional processes in the lower field (He, Cavanagh, & Intriligator, 1996).

1.3. Attentional biases

In studying hemifield differences in normal subjects, it is crucial to minimize any attentional biases that may be present in the experimental situation. There should not be visual or auditory cues, or response factors, that attract the subject's attention to a

particular direction of space, even in the absence of overt eye movement. Attentional biases intrinsic to the display or to the task are often considered in laterality research (e.g. Bryden & Mondor, 1991); but what are rather seldom discussed in published reports are casual asymmetries in the testing environment. Yet in the classical studies of hemifield differences, an experimenter would typically be sitting to one side of the tachistoscope. More recent experiments have used computer-controlled displays, but even in this case there may be distractors such as noises from an adjacent laboratory or simply the sound of the fan in the computer placed to the left or to the right of the experimental monitor. Sometimes an attentional bias could potentially be introduced by the mode of response, as in the experiment of Efron, Yund, and Nichols (1990), where the subject was asked to respond with keys—the arrow keys—that lie at the right of a computer keyboard.

Separate from the problem of exogenous cues is the possibility that the task itself, by engaging one hemisphere disproportionately, may bias endogenous attention to contralateral space (Bryden & Mondor, 1991; Kinsbourne, 1970; Reuter-Lorenz, Kinsbourne, & Moscovitch, 1990; Techentin & Voyer, 2007). In some studies of laterality, a secondary task—e.g. recognition of a small central digit (Davidoff, 1976)—may be used to control fixation, and there is the possibility that this secondary task may similarly bias endogenous attention.

1.4. The present study

In a recent experiment, primarily concerned with the independent issue of how well subjects can compare spatially separated stimuli, we presented pairs of colors that fell at random positions on an imaginary circle centered on the fixation point (Danilova & Mollon, 2006). The subjects were highly practiced and each was tested in multiple experimental sessions. We retrospectively analyzed our data to identify trials on which both targets fell within one hemifield, and we were surprised to find no systematic differences, either between left and right fields or between upper and lower fields.

We have therefore been prompted to carry out the present experiments, which are explicitly designed to detect hemifield differences. Our discriminanda were pairs of colored patches that fell on an imaginary circle of 5 degrees of visual angle centered on the fixation point. The two patches always fell within one hemifield, but we randomly interleaved trials in which the targets fell in the left, the right, the upper and the lower hemifields. The response assignments were designed so that there was no left–right bias when the left or the right field was being tested, and no upper-lower bias when the upper or the lower field was being tested. We attempted to minimize external stimuli that might bias attention. Subjects were practiced and the measured thresholds are near the limits of performance.

1.5. The two subsystems of color perception

Developments in the understanding of color vision give us further reason for looking afresh at the question of hemifield asymmetries in the perception of color. Whereas chromatic information was earlier thought to be carried exclusively by the parvocellular channel of the visual system, color vision is now known to depend on (at least) two independent subsystems, which evolved at different times (Mollon, 2000). The two subsystems remain morphologically, anatomically and immunologically distinct and they project to different layers of area 17. They can be isolated psychophysically (Krauskopf, Williams, & Heeley, 1982).

The phylogenetically ancient subsystem compares the signal of the sparse short-wave (S) cones with some combination of the signals of the middle-wave (M) and long-wave (L) cones. The S-ON

chromatic signal is carried by a morphologically distinct class of ganglion cells, the small bistratified cells (Dacey, 1993; Dacey & Lee, 1994), while an S-OFF signal is carried by a ganglion cell type with a large sparse, monostratified dendritic field (Dacey, 2003). The small bistratified cells (and possibly also the S-OFF cells) project not to the parvocellular laminae of the lateral geniculate nucleus but to the koniocellular laminae, and thence to the superficial layers 2 and 3 of cortical area 17 (Calkins, Tsukamoto, & Sterling, 1998; Hendry & Reid, 2000; Hendry & Yoshioka, 1994). Since this koniocellular subsystem differs anatomically and morphologically from the parvocellular pathway, it is appropriate to consider it separately in any study of asymmetry in color perception. But there is an additional reason to check for upper/lower field differences in this subsystem: in some non-primate species of mammals, marked differences have been found between upper and lower fields in the numerosity of short-wave cones (Szél, Lukáts, Fekete, Szepessy, & Röhlich, 2000).

The second subsystem of color vision is thought to be phylogenetically recent and may have arisen from the duplication of a gene on the X-chromosome in ancestral primates (Hunt et al., 1998; Nathans, Piantanida, Eddy, Shows, & Hogness, 1986). It depends on the comparison of the rates of photon absorption in the long- and middle-wave cones. This chromatic signal (L/M) is thought to be carried by the midget ganglion cells, which project to parvocellular layers of the lateral geniculate nucleus and thence to layer 4 of cortical area 17 (Derrington, Krauskopf, & Lennie, 1984).

In the present experiments, we set out to test the two subsystems independently. Subjects were required to discriminate the chromaticities of two stimulus patches that differed either in the phylogenetically older S-cone signal or in the phylogenetically recent L/M signal.

2. Methods

2.1. Apparatus and stimuli

Stimuli were presented on a Sony Trinitron 21-inch monitor (GDM-F500) and were generated by a VSG 2/5 graphics board (Cambridge Research Systems), which allowed a precision of 15 bits per gun. The refresh rate of the monitor was 80 Hz. Subjects viewed the screen binocularly from a distance of 57 cm. Their eyes were level with the center of the screen.

A steady background field was always present: its chromaticity was equivalent to that of equal-energy white and it had a CIE luminance of 10 cd m^{-2}. The discriminanda were sectors of an annulus, and their centers lay on an imaginary circle that had a radius of 5 degrees of visual angle (see Fig. 1). The width of each target sector at its midpoint was 2 degree of visual angle and its radial length was 2 degrees. The duration of the targets was 100 ms, a value chosen to be too short to allow eye movements during the presentation.

The position of each target was specified by its position on the imaginary circle relative to 12 o'clock (we indicate these positions with the degree symbol (°) in order to distinguish them from visual angles). Relative to 12 o'clock, there were four cardinal positions that constrained where targets could fall, 45°, 135°, 225° and 315°, but the actual position was randomly jittered and could fall with equal probability at any integer position in the range ±15° of the cardinal position. However, the separation of the two targets was constrained always to be 90°. When the right visual field was being tested, the cardinal positions were 45° and 135°, when the left field was tested, 225° and 315°, when the upper field was tested, 45° and 315°, and when the lower field was tested, 135° and 225° (see Fig. 1). Thus the same retinal positions are probed equally often whether the test stimuli are both presented to one cerebral hemisphere (the left or right hemifield cases) or whether they are presented to different hemispheres (the upper or lower hemifield cases).

We represent our stimuli in a chromaticity diagram (Fig. 2), designed to be analogous to the diagram of MacLeod and Boynton (1979) but constructed from the 10-deg cone sensitivities of Stockman and Sharpe (2000). The latter sensitivities are appropriate for our parafoveal targets. To retain the familiar structure of the MacLeod-Boynton chromaticity diagram, we have scaled the Stockman and Sharpe 10-deg L and M cone fundamental sensitivities to have the same relative heights as the 2-deg fundamentals of Smith and Pokorny (1975), which were used to construct the original MacLeod-Boynton diagram. As an analog of Judd (1951) luminance, which was used for the original diagram, we took the sum of the scaled long-wave and middle-wave signals (L + M). The referent and variable stimuli had on average the same value of (L + M) as the background field, but on any given trial the luminance of the two patches were independently jittered in the range ±5% of the average value, in order to ensure that subjects did not use luminance cues to solve the task. Calibrations were performed with a Spectrascan 650 spectroradiometer.

2.2. Procedure

Within each block of trials, all four hemifields were tested in a randomly interleaved sequence. Thresholds were measured by a 2-alternative spatial forced choice. In Experiment 1, the two stimuli differed in the short-wave cone signal, and in Experiment 2, they differed in the ratio of the long- and middle-wave cone signals. On each trial, one of the stimuli, chosen at random, was conceptually the reference stimulus and one was the variable stimulus. The S signal (Experiment 1) or the L/M ratio (Experiment 2) was greater in the case of the variable stimulus, and the subject was required to identify this stimulus. It was important to ensure that the subject actively compared the two stimuli on every trial, since practiced subjects, in a discrimination experiment where the referent stimulus is fixed, may achieve high performance by making absolute judgments of just one of the two stimuli (Lages & Treisman, 1998). To oblige our subjects to compare the two stimuli, we therefore jittered the chromaticity of the referent stimulus from trial to trial over a range of 25 finely-spaced steps (Danilova & Mollon, 2003, 2006). In Experiment 1, the L/M chromaticity coordinate of the referent was fixed at 0.70 and the S value varied from 0.0091 to 0.0125 (see Fig. 2). In Experiment 2, the S value was fixed at 0.0017 and the L/M coordinate varied in the range 0.643 to 0.679. In both cases, we chose the set of referents to lie in a range where we knew the Weber fraction to be approximately constant (Danilova & Mollon, 2006): this allowed us to alter the Weber fraction according to a staircase routine (Cornsweet, 1962) while nevertheless the referent varied from trial to trial.

For each of the four hemifields independently, the percentage difference between the referent stimulus and the variable stimulus was adaptively adjusted across trials according to the following 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 of the staircase was 10% of the difference between test and referent. All four staircases continued until at least 15 reversals had been accumulated on each staircase. Data from the first five reversals of each staircase were discarded, and the subsequent reversals were averaged to give an estimate of the threshold for that particular hemifield. In Experiment 2, each subject completed 12 independent experimental runs, each taking 10–20 min and usually spread across several different test days; the first 2 runs were treated as training and the last 10 runs were used for data analysis. This was also the case for Experiment 1, except
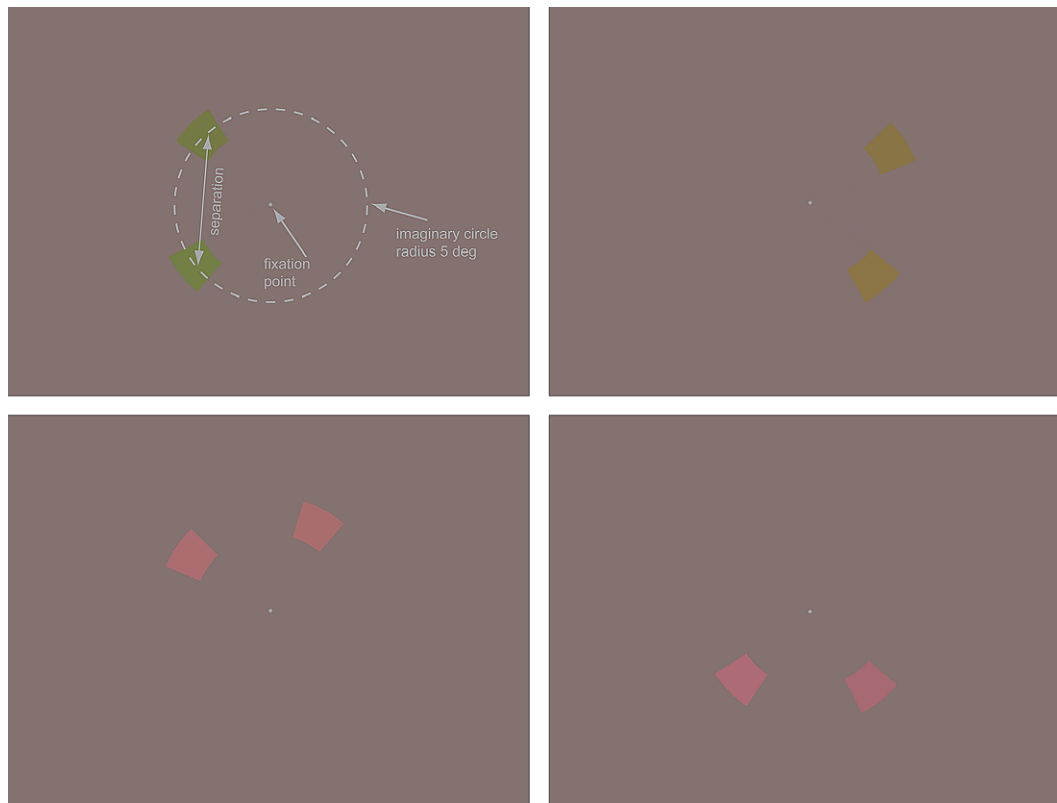
Fig. 1. Examples of the stimuli used in the experiments. The centers of the two stimulus patches lie on an imaginary circle indicated by the broken line in the upper-left panel. One stimulus, chosen at random, is the referent stimulus and the other is the test or variable stimulus. On any trial, the two stimuli are 90° apart on the imaginary circle and always fall within one hemifield (left, right, upper, lower). A central fixation point is continuously present. The upper two panels show examples of test stimuli on the *L/M* axis of color space and lower panels show examples of test stimuli on the short-wave axis.
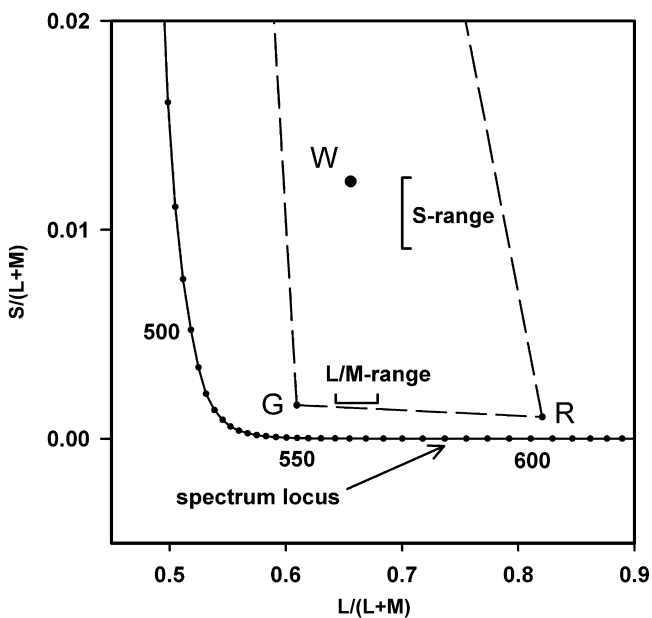
Fig. 2. Chromaticity diagram representing the ranges used for the referent stimuli in Experiments 1 and 2. The diagram is an analog of the standard MacLeod-Boynton diagram, but is constructed from the 10-deg Stockman-Sharpe fundamentals. G and R denote the chromaticities of the green and red phosphors of the monitor and the dashed lines delimit the gamut of the possible colors that the monitor can produce. W indicates the chromaticity of the background field., which was equivalent to equal-energy white when plotted in this space.

that one subject completed 11 experimental runs and we based the analysis on the last 9 runs.

Subjects responded by means of four pushbuttons, arranged in a diamond on a small, hand-held response box. On trials on which the left visual field or the right visual field was being tested, the subject responded with the upper or lower button to indicate whether the upper or lower target was bluer (Experiment 1) or redder (Experiment 2). On trials on which the upper visual field or the lower visual field was being probed, the subject responded with the left or the right button to indicate whether the left or the right target was the variable target. Thus, the responses were very compatible with the spatial arrangement of the stimuli. Most importantly, when left or right fields were tested, the responses did not introduce a left–right bias, and when upper or lower fields were tested, the responses did not introduce an up-down bias. After each trial, a tone signal gave the subject feedback as to the accuracy of his or her responses. The next trial followed the subject's response by 1 s. Subjects were not told to respond as quickly as possible, but we routinely recorded their response times.

The experiment was conducted in a quiet, darkened room and we endeavored to eliminate visual or auditory cues that might bias the subject's attention. The host computer was placed symmetrically behind the display monitor. Subjects were instructed to fixate the central fixation point before each trial.

2.3. Subjects

There were 10 volunteer subjects, 5 female and 5 male. All were dextral adults, the average age of the females being 37.8 and that of the males, 37.4. All had normal color vision, as tested by the Ishihara plates (9th edition) and the Cambridge Color Test (Regan, Reffin, & Mollon, 1994). Subjects gave informed consent.
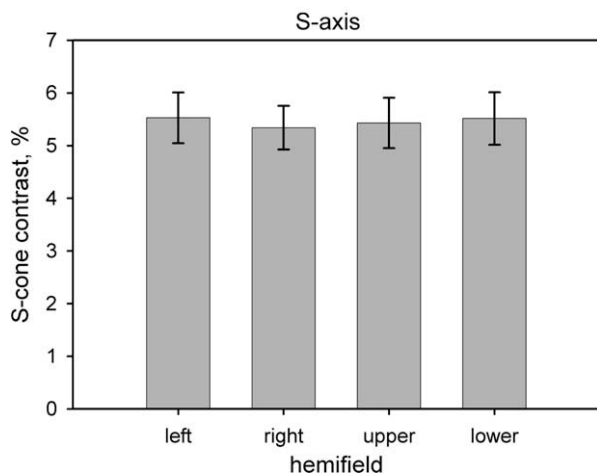
Fig. 3. Thresholds for S-cone discrimination in the four hemifields. The values shown are averages from 10 subjects. Error bars correspond to ±1 SEM and are based on inter-subject variability. Probing of the different hemifields was fully randomized within each experimental block of trials.

3. Results

3.1. Experiment 1: discriminations based on comparison of S-cone signals with L and M cone signals

The average thresholds from the four conditions of Experiment 1 are shown in Fig. 3. The error bars are based on inter-subject variance and represent ±1 SEM. The absolute values of the thresholds are of the order of 5%, a magnitude typical for this axis of color space when subjects are practiced (Danilova & Mollon, 2006; Wyszecki & Stiles, 1967, Table 7.4). It can be seen from Fig. 3 that the thresholds for different hemifields are very similar. A one-way repeated-measures ANOVA was performed on the subject means with hemifield as a factor with four levels. There was no significant effect of hemifield ($F(3) = 0.504$).

Since 10 separate estimates were available for each threshold for each subject, we also performed one-way ANOVAs for the individual subjects. Only one male subject showed a significant effect of hemifield ($F(3) = 3.1$, $p = 0.039$) and pairwise comparison with Bonferroni correction showed only one significant difference: his upper visual field exhibited poorer performance than his right field.

Although our task was not a speeded one, it is of interest to consider response times for opposite hemifields. Our experimental design has the advantage that the two possible responses (i.e. up vs. down or left vs. right) are not confounded with hemifield (i.e. left/right or upper/lower): for opposed hemifields, each of the two possible responses occurs with the same frequency. Average response times for left and right hemifields were 826 and 818 ms, respectively. This small difference is opposite in direction from that expected from a right-hemisphere superiority and is not statistically significant ($t = 0.9$). The values for the upper and lower hemifields were 806 and 779 ms, respectively, this difference was not significant ($t = 1.71$).[1]

In addition to asking whether the left and right hemifields differ, or the upper and lower hemifields differ, we can ask whether performance is poorer according to whether the chromatic dis-

crimination requires transmission of information from one hemisphere to the other. To address this question we can average the thresholds for the left and the right hemifields (cases where the comparison can in principle be made within one cerebral hemisphere) and compare these with the average of the thresholds for the upper and lower hemifields (cases where transmission between hemispheres is obligatory if the two stimulus patches are to be compared). The design of our stimulus array has the advantage that the same retinal areas are probed equally often in the two cases. The averaged thresholds for the intra-hemispheric and inter-hemispheric cases are shown in the upper panel of Fig. 5. A *t*-test showed no significant difference between the two values ($t = 0.26$).

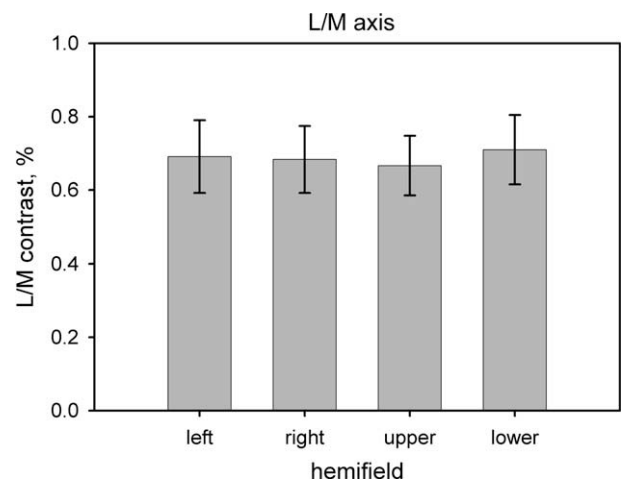### 3.2. Experiment 2: discriminations based on comparison of L and M signals

Fig. 4 shows, for each of the four hemifields, the mean thresholds on the *L/M* axis of color space. The absolute values of the thresholds are under 1%, as would be expected for discriminations on this axis by trained subjects (Danilova & Mollon, 2006). As in the case of the *S* axis, the thresholds for different hemifields are very similar. A one-way repeated-measures ANOVA showed no significant effect of hemifield ($F(3) = 0.815$).

We also analyzed L/M thresholds for each individual subject. One-way ANOVAs showed significant but inconsistent effects for three female subjects. For subject MD, $F(3) = 4.77$ ($p = .007$) and pairwise comparisons with Bonferroni correction showed that the upper visual field was poorer than all other visual fields. For IK, $F(3) = 3.36$ ($p = 0.03$), and pairwise comparison showed that the lower field was poorer than the right. For ED, $F(3) = 3.5$ ($p = 0.025$) and pairwise comparison showed the right visual field to be poorer than the upper. In no individual case was there a significant left–right difference.

Average response times for the left and right hemifields were 748 and 756 msec, respectively, this difference, in favor of the right hemisphere, was not significant ($t = 0.66$). The values for upper and lower hemifields were 718 and 706 ms, respectively ($t = 1.12$, n.s.).

In the same manner as for the *S* axis of color space, we compared L/M thresholds for the intra-hemispheric and the inter-hemispheric cases, combining left and right fields for the former case and upper and lower fields for the latter case (Fig. 5, lower panel). A *t*-test showed no significant effect ($t = 0.11$).

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[1] We have subtracted 3 ms from the recorded values for the lower field, to allow for the fact that targets lower on the screen of a CRT are plotted later in the raster scan than are targets higher on the screen. Each frame of our display occupies approximately 12 ms and the average spatial separation of our upper and lower targets is approximately $\frac{1}{4}$ of the total screen height.
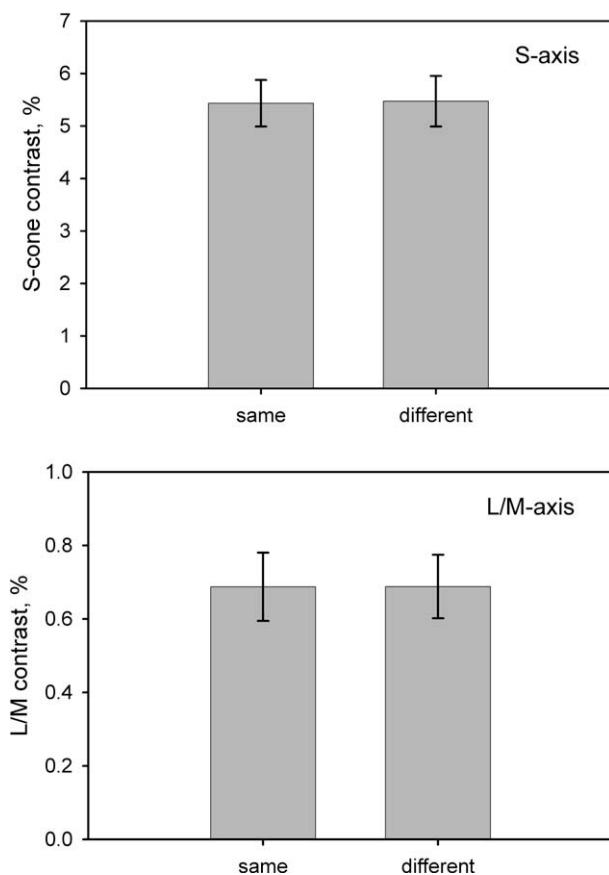

Fig. 4. Thresholds for *L/M* discrimination in the four hemifields. The values shown are averages from 10 subjects. Error bars correspond to ±1 SEM and are based on inter-subject variability.

Fig. 5. Average thresholds for the case where the stimuli are delivered to the same hemisphere and the case where they are delivered to different hemispheres. The upper panel shows results for the *S* axis, the lower panel for the *L/M* axis. Error bars correspond to ±1 SEM and are based on inter-subject variability.

4. Discussion

4.1. Failure to find significant hemifield differences in color discrimination

Neither our average results, nor those for individual subjects, replicate the right-hemisphere advantage previously reported for chromatic discrimination at an eccentricity similar to that used here (Davidoff, 1976). This was true for both subsystems of color vision. Two main factors may explain why we fail to find the significant asymmetry found by others:

4.1.1. Attentional bias

In order to avoid biases of attention, we took care to render our testing conditions as symmetrical as possible. This applied not only to the auditory and visual environment, but also to the mode of response. In addition, on half the trials at random, the discriminanda were symmetrically placed across the midline, and this may have discouraged the emergence of strong biases to left or right.

It is curious that papers on hemifield differences seldom report that precautions were taken to ensure the symmetry of the auditory and visual testing environment. We recommend that such precautions should be standard.

In hemifield studies, an asymmetry of attention may also be introduced because the primary or secondary task occupies one particular hemisphere and thus biases attention to contralateral space (Cohen, 1982; Kinsbourne, 1970). In this context, we note that we did not introduce a secondary task and the continuous variation in our stimuli may have minimized verbal labeling. It is rel-

evant that Fonteneau and Davidoff (2007) found no left-right asymmetry in an implicit color task using event-related potentials.

4.1.2. Degree of practice

Our subjects were extensively practiced and received feedback on each trial. In absolute values, their thresholds compare favorably with values published in the psychophysical literature. Thus the subjects were discriminating near the limits of human performance. Sasaki et al. (2007) remark that 'in a visual half-field paradigm, visual field differences sometimes disappear with practice' and they themselves ran subjects for only 30 trials, but they give no rationale for preferring the data of the untrained subject. We believe that the limiting properties of each hemisphere are better revealed by the performance of highly practiced subjects than by responses made at the very earliest stage of practice. When asked to compare the chromaticities of parafoveal stimuli, untrained subjects may need a period of calibration with feedback before they can consistently relate the signals available from different retinal points (Mollon & Danilova, 1996)[2]

A secondary advantage of using practiced subjects is that multiple independent measurements are available for each subject and thus statistically valid judgments can be made about the presence of hemifield differences for individuals.

4.1.3. Hemifield differences for color discrimination: Conclusion

When thresholds are measured with trained right-handed subjects and when care is taken to minimize asymmetries in the testing situation, our results show that the intrinsic neural limits to chromatic discrimination are similar for the two hemispheres.

Our conclusion must necessarily be limited to the experimental conditions that we have used, and a different result might be found in a speeded task such as that of Sasaki et al. (2007). However, the accumulated evidence suggests that there are no robust differences between the left and right visual fields in basic sensory functions. Negative results have been published for contrast sensitivity and for the discrimination of orientation, contrast and spatial frequency (e.g. Danilova & Mollon, 2002; Fendrich & Gazzaniga, 1990; Kitterle & Kaye, 1985; Magnussen, Landrø, & Johnsen, 1985).

From an ecological viewpoint, this symmetry of sensory apparatus is to be expected: in the natural world, the average distributions of chromaticities, orientations and spatial frequencies, and the rates of optic flow, should be nearly identical in the left and right fields, and so it would in fact be odd if man's sensory apparatus exhibited a left-right asymmetry.

From the ecological standpoint, there is much more reason to expect sensory differences between upper and lower hemifields than to expect them between the left and right hemifields: the upper and lower fields clearly do differ in their average stimulation, notably in the distributions of luminance, spatial frequency and optic flow (Previc, 1990)—and probably also in chromaticity. A lower-field superiority for color discrimination has in fact been reported by Levine and McAnany (2005). Yet we ourselves find no consistent difference between upper and lower fields. Even when discrimination depends on the signals of the short-wave cones—which exhibit clear anisotropies in some mammals—our results show no advantage for the lower field.

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[2] It is noteworthy that, under conditions of uniform adaptation, a target of a given chromaticity has a similar appearance wherever it falls in the parafovea, even when the subject is untrained. This spatial constancy is so nearly complete that it is commonly taken for granted by visual scientists themselves, and the question of how it is maintained is seldom asked. Yet the human lifespan offers no opportunity to send the system back to the factory for recalibration. There must be some active calibration process that maintains spatial constancy over the observer's lifetime, presumably by monitoring signals as everyday objects pass across the visual field.

4.2. Intra- vs. inter-hemispheric stimulation and the site of comparison

Decisions about compared colors must ultimately be made at a single locus. In one possible model, the decision would be made in a 'color center' located in pre-striate cortex, e.g. at one of the sites identified as color selective by McKeefry and Zeki (1997) or Brewer et al. (2005). Even if the color center were bilaterally represented, transmission of information across the corpus callosum would be required when the stimuli fell in opposite fields, and degradation could in principle occur during this transmission. In fact, our results show no difference in thresholds according to whether the two discriminanda initially arrive in the same hemisphere or in different ones.

This finding is not unexpected if a different hypothesis is adopted for the site of comparison. We have suggested elsewhere that the comparison of spatially separated colors depends not on hard-wired 'comparator units' drawing inputs from the two corresponding positions, but rather on symbolic codes that can be transmitted over a 'cerebral bus' (Danilova & Mollon, 2003, 2006). The actual comparison may in fact be performed at a site in one or other pre-frontal cortex, and to reach this site all chromatic information—whether it originates in the same hemisphere or the opposite one—has to be carried there by white matter. A recent study using diffusion tensor imaging (Sherbondy, Akers, Mackenzie, Dougherty, & Wandell, 2005) shows that the inferior occipito-frontal fasciculus of each hemisphere contains not only a component that originates in the ipsilateral occipital lobe but also a second component that originates in the contralateral occipital lobe and passes through the posterior corpus callosum. If sensory decisions are in fact made in the pre-frontal cortex, then the same number of synapses may be involved in inter-hemispheric and intra-hemispheric comparisons. In that case, no more degradation of information would be entailed in the one case than in the other.

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