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STAGES FOR EXTRACTING COLOUR INFORMATION: HOW THE BRAIN PROCESSES COLOUR*

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Colour information is processed by many stages in the visual system. Primate colour vision relies on three photoreceptors, cones, which sample visible light and send signals to the second stage, cone–opponent units. Surprisingly this stage determines not only the threshold detection for chromatic patches, but also matching surface colours under various illuminations. Hue discrimination at detection thresholds reveals contribution of the third stage, colour-opponency, which determines colour categories, or unique hues. These hues remain constant for para-central, peripheral field locations, providing the reference for veridical vision. However, more challenging tasks of colour identification require contributions from higher colour centres (V4–complex, TEO, IT).

The aim of this study is to present key experiments illustrating the contributions of the cone opponent stage and unique hues in low-level colour vision, whereas the effect of damage to various stages will be discussed in terms of the distributed representations in the visual system.

The experiments showed that the colour apparatus uses signals derived from the entire visual field (i.e. panoramic viewing), perhaps using some form of spatial and temporal integration. This observa-

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tion is supported by the fact that when a matching paradigm is used to compare peripheral and central colour samples, peripherally invariant hues correspond to unique hues. And, finally, there is a trade-off between sensitivity and selectivity, and it seems likely that neurons form flexible assemblies which can act together to extract either hue, giving fine hue discrimination but poor sensitivity, or extract contrast giving high chromatic sensitivity but having poor hue discrimination.

Key words: *colour constancy, colour matching, cone contrast, unique hues, distributed representations.*

Running Head: *How the brain processes colour*

Introduction

Primate vision developed to extract critical information from the luminance distribution on the retina. Up to about 90% of total sensory information is visual. At first glance, the visual system consists of several processing stages and parallel pathways. In spite of many interactions between the stages, it will be shown that these can be identified by choosing appropriate experimental conditions.

Colour vision is a relatively recent addition to mammalian vision. Its aims are at least dual: (1) to signal an object's identity and characteristics on the basis of light reflected from its surface (e.g. ripe, fresh, or rotten fruit), (2) to facilitate differentiation precursor to identification of objects by their colour contrast (i.e. breaking their camouflage). These two aspects – accurate or stable perception of colours and the ability to identify objects by their contrast – are arguably served by different mechanisms and possibly different subsets of neurons in the visual system. Computationally, maintaining constant colour vision under many different lighting conditions is extremely complex but seems to be achieved by visual systems effortlessly. This phenomenon has been described as colour constancy. Strictly, 'colour constancy' means that perceived surface colours should be invariant under variable illumination (Arend and Reeves, 1986), which refers to the mechanism (1) mentioned above. Conversely, 'relational colour constancy' (Foster and Nascimento, 1994) may be determined as the ability to recognize that a given scene consists of the same objects under variable illumination or that the objects within a scene change. In this situation, mechanism (2) operates.

All colour processing is carried out in the retina and geniculo-cortical pathway. The most important retinal stages of normal trichromatic colour vision are: 1) cone photoreceptors – cones sensitive to short (S), medium (M) and long (L) wavelength; 2) interactions between cones are basically linear, leading to cone–opponent mechanisms, L–M and S–(L+M), mediated by ganglion cells extracting cone contrasts. In addition, there are many visual cortical areas, probably more than 30. Those especially important for colour are V1, V2, V4–complex and temporal cortex (for review, see Zeki, 1990).

Basic definitions: Cone contrast, unique hues, CIE1931 xy colour plane, constancy index

Cone contrasts are defined as the relative differences in activation of cones by sample and background. Thus, for L-cones the L-cone contrast is calculated as

$$C_L = \frac{(L_{sample} - L_{background})}{L_{background}}$$

and similarly for M- and S-cones.

These cone contrasts are components of contrast between samples and backgrounds that will be shown to remain constant according to the famous von Kries rule.

There is a continuum of discernable colours, amounting to over 1000 up to 2 million. Colour plate 1 illustrates this continuum in the CIE1931 xy colour space. Some hues are called unique hues: red, green, blue and yellow, which serve as markers for colour perception by dividing the continuum of colours into a few well defined categories (Mullen and Kulikowski, 1990).

Unique hues are defined as not containing any components of adjacent hues. Thus, unique blue does not contain any appearance of either green or red-purple, unique red contains neither blue-purple nor yellow, unique yellow neither red nor green, and unique green neither yellow nor blue. They are marked on the CIE1931 xy colour plane in Colour plate 1.

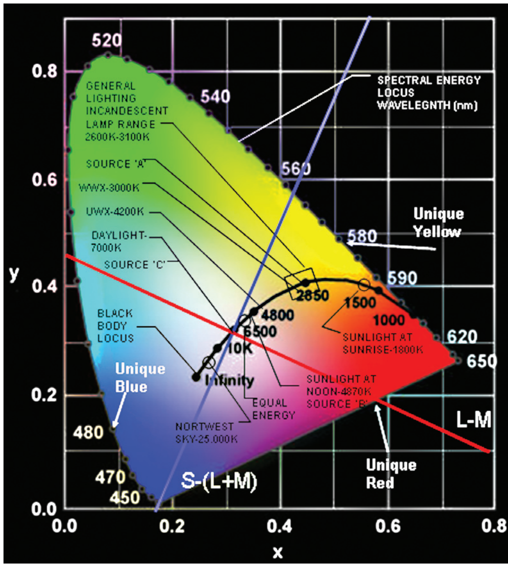
As stated above, colour constancy means that the appearance of surface colours should remain constant under various illuminations. Physics can retrieve the information about surfaces, if the illuminant properties are known (Parkkinen et al., 1989). How can the visual system implement this transformation? The present evidence suggests that different stages and channels, which may interact and merge, are used. The characteristics of these mechanisms can be experimentally isolated. In order to assess colour constancy quantitatively, the Brunswick Ratio (BR) is often used:

$$BR = 1 - \frac{\text{perceived shift}}{\text{physical shift}}.$$

This expression indicates how perceived shift is compensated compared with physical shift due to an illuminant change. It shows that BR = 1 corresponds to full constancy and BR = 0 corresponds to zero constancy. A tacit assumption is that the distances are using a uniform scale. The CIE u'v' plane is commonly chosen because it is regarded as a reasonable approximation to a perceptually uniform colour space (see Figure 2). For demonstration purposes the CIE xy plane is preferred, as it shows the whole gamut of visible colours (Colour plate 1).

Colour Plate1 & Colour Plate2
on the opposite page

The L–M and S–(L+M) cardinal cone-opponent axes are indicated as red and blue lines respectively (Colour plate 1). The locus of the different phases of daylight is close to the black body locus. Source C is standard daylight illuminant, and source A mimics afternoon sunlight. Infinite colour temperature (S) is the opposite extreme. Unique blue and yellow (arrowheads) are close to the daylight locus. Unique green appears near the apex of this colour space and has been shown to be more variable than the others. These two post-receptor systems, cardinal axes and unique hues are modelled by separate equations. In gross simplification, we may consider that the cone-opponent mechanism based on the cardinal axes is specialised for detection, being highly sensitive to small changes in chromatic contrast. On the other hand, hue categorization is specialised for selectivity which is essential for hue discrimination as described in K. T. Mullen and J. J. Kulikowski (1990). Depending on task and specific viewing conditions, these two basic mechanisms may be involved to different degrees in any given task, as will be shown in two different types of matching experiments described below.



Colour plate 1

The CIE 1931 xy chromaticity plane representing all colours. The Planckian curve (black body locus) approximates daylight illuminations. Cardinal axes L–M (red) and S–(L+M) (blue) indicate cone opponent stimulation. Additionally, unique blue, unique red and unique yellow are indicated by the arrows. Unique green is near the apex.

Illuminant C	Illuminant A White looks beige	Illuminant G White looks greenish

Colour plate 2

This plate consists of three parts, which should be initially viewed separately in succession. The pictures show a girl seen against a natural background with a white surface in the foreground. The scene is illuminated by either standard white (daylight C, left) the tungsten–like illuminant A (an afternoon sunlight, middle) or an artificial green light (right). Note that persistent viewing of each part hardly improves colour perception.

The different contributions of the colour processing stages

Stage 1. Cone photoreceptors

If a uniform surface is viewed on a black background, its perceived colour depends only on light reflected from its surface. Here, colour is determined solely by cone excitation and therefore wavelength composition. In this case, no other information is available, and this situation is sometimes referred to as 'vision in the void'.

Stage 2. Cone-opponency

Colour appearance depends on the context and the background. When even a narrow background is seen, e.g. through a keyhole, this kind of *local viewing* substantially helps to estimate surface colours, while the illumination changes, by extracting colour contrast information. A century ago, von Kries made some observations which in contemporary terms mean that objects' colours are matched according to their L-, M- and S-cone contrasts (see Foster and Nascimento, 1994). This effect is illustrated by Colour Plate 2 a, b, c where a girl is seen against a natural background behind her and a white surface in front of her. The scene is illuminated by either standard white (daylight C, left) the tungsten-like illuminant A (an afternoon sunlight, middle) or an artificial green light (right). We can understand that this is the same girl differently illuminated, because we view the overall situation. But it is obvious that specific colours do not match; especially the lower panel of the frame betrays different illuminations. Thus, colour constancy is poor, i. e. perception is influenced by the illuminant and, for example, white looks beige or green.

However, the overall appearance of colours improves if a scene is viewed not by the observer standing in daylight and peeping through a restricted gap (e.g. a keyhole), but through a large open window or entering a room (panoramic viewing). After one minute colours seem natural, even though they are not quite veridical. This effect is well recognized by some shoppers who prefer daylight viewing when trying to judge the colour of garments or other items. There is a clear paradox; cone-opponency is retinal, and that is why hasty conclusions often describe colour constancy as a retinal process.

Stage 3. Unique hues and colours

It is important to have some mechanism(s) which extract veridical colour information, and obvious candidates are colour-specific neurons in the visual cortex. Such units, tuned to unique hues (Valberg, 2001; Neitz J. and Neitz M., 2008), could serve as markers for colour perception.

According to the present views, the extraction of colour information begins after the cone-opponent stage. However, it may be argued that colour-specific units may be located in the LGN and operate in parallel or in the primary visual cortex V1 or in V2 (Yoshioka et al., 1996). Certainly, there are some well organized structures in the inferior temporal cortex (IT), which appear to extract unique hues, but it remains unknown how the signal reaches this target (Stoughton and Conway, 2008). However, lesions in the colour area V4 complex do not disrupt information about hues (Walsh et al., 1993). It seems that another theory must be considered, – for example, that of distributed representations.

This paper presents two series of colour-matching experiments: (1) matching under different illuminations that could be explained mainly by the mechanism of cone-opponency and (2) peripheral colour matching that shows mainly contributions of unique hues. However, experiment (1) shows additional weak influences of unique hues, whereas experiment (2) shows some influence of cone opponency. This 'cross-talk' is difficult to reconcile with the familiar 'trigger-features' concept of units signalling one specific feature. It seems that neurons in the visual cortex may be used more flexibly, and their contributions to different tasks may be determined by the balance of their sensitivity and selectivity that is consistent with the concept of distributed representations (Lehky and Sejnowski, 1991, Vaitkevicius et al., 1984). This concept is even more important when interpreting some effects of lesions in visual cortical areas, which cause a range of partial colour deficiencies.

Methods

Two series of experiments are described:

1) colour matching; effects of different illuminants, effects of adaptation time and field size;
2) colour matching; effect of retinal eccentricity.

Experiment 1. Asymmetric colour matching

Our experimental methods with simulated colours on a display have been described previously (Murray et al., 2005, 2006a, 2006b, Daugirdiene et al., 2006). Here we provide only essential details. All experiments were conducted in a darkened room. The stimuli were generated with a VSG card (Cambridge Research Systems, Rochester, UK) and presented on a high resolution colour monitor. The screen was viewed from 30 cm using a head and chin rest. A box (75 × 75 × 100 cm) enclosed the front of the monitor to exclude extraneous light. In some experiments, a slightly conical tube was used in order to increase the view field from 20° to 120°, as described below. Subjects had normal colour vision according to the Farnsworth 100 Hue and Moreland tests and normal visual acuity.

Simulated Munsell samples were used in a successive asymmetric colour matching task. The Munsell samples were classified in terms of hue, value (luminance) and chroma (saturation). They were simulated using Parkkinen reflectance functions to reflect the light from each chip under the different illuminants (Parkkinen et al., 1989). Three basic functions were used (Oxtoby and Foster, 2005). The luminance of the neutral background was 20 cd/m^2 under all test illuminants. Munsell samples 7/4 (value 7, chroma 4) on a neutral background (N7) were used. The set consisted of the following sequence: 10P, 10PB, 10B, 10BG, 10G, 10GY, 10Y, 10YR, 10R and 10RP. All ten Munsell samples were presented in the centre of the screen, subtending 2°, while the surrounding neutral background (N7) subtended 20° (Figure 1 left and middle panel).

To evaluate the colour shift of the neutral background under the two test illuminants A and S, test stimuli composed only of the neutral background N7 illuminated by one or the other test illuminant were used. The subject adjusted the hue, saturation, and brightness of the sample to match the apparent colour of the back-

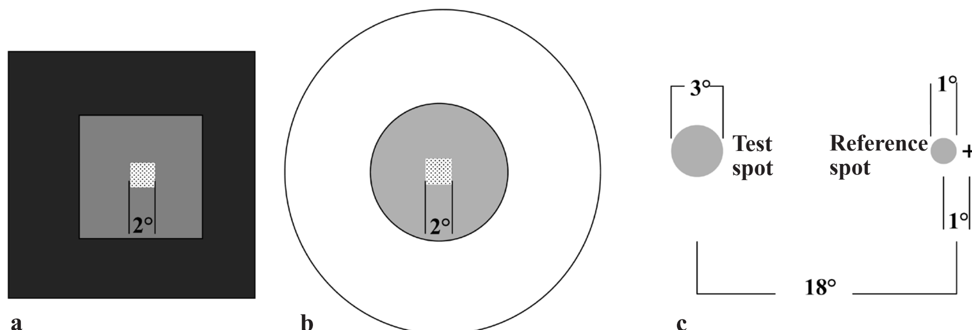


Figure 1. ***Stimulus configuration for the three experimental setups.***

Left panel: The reference and test samples (2°) were surrounded by a 20° neutral background (value 4) and presented sequentially for 1s under reference illumination C, or test illumination A. The sample presentation was always preceded by neutral background presentation for the same duration (1 s). The area outside was dark.

Middle panel: Stimuli as in (a), but additionally the samples and the background were surrounded by a white tube, which resulted in a field of 120°, reflecting either reference or test illumination. The stimulus presentation time was either 1 s or 60 s.

Right panel: Asymmetric colour matching of a 1° para-fovea reference sample with a 3° test sample at 18° eccentricity. The reference sample was varied in 15° steps in colour space, and the observer matched the test with the reference sample changing hue, saturation and luminance.

ground under the same timing conditions as described above (see Figures 3, 4 and 5 for these background shifts).

The overall strategy of these experiments was to maintain adaptation to illuminant C. After an adaptation period of 60 s, on the neutral background the sample appeared against the test illuminant background, for a variable period between 1, 5, 30 and 60 s. Following a corresponding 1, 5, 30 or 60 s re-adaptation (or top-up) period to illuminant C, the sample re-appeared under illuminant C. The subject then adjusted the hue, chroma, and value of the sample under standard illuminant C to match it as it had appeared under the test illuminant. The role of the top-up period was to maintain adaptation to illuminant C, especially for the longer durations. The matching time was not restricted, so that the presentation cycle could be repeated until the subject indicated that he / she had obtained a satisfactory match.

Overall six test illuminants were used. Two Planckian illuminants, which were chosen to simulate natural viewing conditions, illuminant A (2856K; u' = 0.256, v' = 0.524) and illuminant S (u' = 0.174, v' = 0.392), are presented in this report. Data for all illuminants (Figure 2) are reported in A. Daugirdiene et al. (2006).

In another experiment, we studied the effect of a double change in test illumination. The reference illuminant was now A, whereas the test was illuminant S, which is at the end of the Planckian locus corresponding to a very high temperature of the black body (over 30000 K).

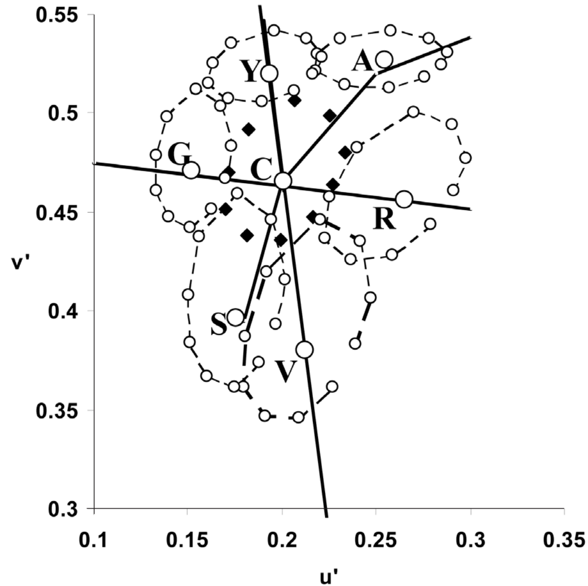


Figure 2.
The CIE 1976 chromaticity coordinates (u'v') of the colour stimuli. Illuminant C was used as a reference illuminating a neutral background (N7, see the central point). The chromaticities of 10 reference samples are indicated by filled circles. Test stimuli consist of the same 10 samples (small empty circles) on the same neutral background under test illuminants: A and S (Planckian) and cardinal G, R, Y, V (large empty circles). Thick continuous lines are: cardinal-tritanopic (vertical), cardinal red-green (horizontal) and the Planckian (oblique curve). Note that the cardinal illuminants (G, R, V, Y) are to make the loci of the test samples tangent to the locus of the reference samples. This means, for example, that the cardinal red sample under the test illuminant G reflects the same light as does the cardinal green sample under C.

Small (20°) and large (120°) background field sizes

In order to test the effect of field size, two viewing conditions were devised: a 20° field and a 120° field (Figure 1 left and middle panel). Despite the dim conditions, the subjects were aware of the surroundings of the monitor with the 20° background. To eliminate these factors and to increase the field of view, the background and the test stimulus were viewed through a slightly cone-shaped tube constructed from matt white stiff cardboard. The base of the cone was fixed to the front of the monitor and had the same diameter as the adapting background of 20º. It was carefully attached to the head rest so that there was no light leakage around the subjects' forehead or temple. The surface of the paper diffusely reflected the display so that the subjects' entire visual field consisted of a continuous surround having the same chromaticity as the background. In these measurements, only the stimulus and the background remained in the subjects' field of vision. In a sense, this is a type of Ganzfeld, having the benefit of adapting the entire field of view of approximately 90° temporally and between 40° and 60°

nasally, depending on the facial anatomy. We estimate that this produces, on average, a binocular field of view of approximately 120°, and we have labelled the figures accordingly (Figure 1 middle panel).

The procedure for the 120° field experiment was the same as in the 20° field, except that an additional adaptation period of 60 s was used. To reiterate, note that readaptation periods were always matched by presentation periods, so that, for example, 60-s presentation was followed by 60-s re-adaptation to illuminant C.

Data analysis

The data are presented by evaluating perceptual and physical changes of chromaticity co-ordinates in CIE1976 Lu'v' colour space, using a single dimension variation of the Brunswik Ratio (BR).

Experiment 2.
Peripheral colour matching

The equipment and the experimental procedure were described previously by N. R. Parry et al. (2006). Briefly, stimuli were generated by a ViSaGe (Cambridge Research Systems©) visual stimulus generator on a Sony© Trinitron® Muliscan520GS monitor which was calibrated by a PR650 SpectraScan© Colorimeter (Photo Research Inc.) and a ColourCal© Colorimeter (Cambridge Research Systems, Rochester, UK).

Two subjects, whose colour vision was normal, were used in these experiments. Both of them showed a preference for unique red away from the average (data are shown only for TP). The colour matching experimental procedure was an asymmetric colour matching paradigm first described by N. R. Parry et al. (2006). The subject had to fixate on a fixation cross, and two spots, the reference and the test, were presenting simultaneously for 380 ms. The reference spot (1° diameter) was presented 1° from the fixation point. The test spot (3° diameter) was presented at 18° eccentricity. The hue of the reference spot was changing from 0° to 360° with 15° steps, and the saturation was always at 0.5 (for details in colour space used, see Parry et al., 2006). The task for the observer was to match the reference and the test spot in terms of hue and saturation with a response box, changing the chromaticity of the large spot (Figure 1 right panel).

Unique hues were determined using a four alternative forced choice method. A 3° spot was presenting on the monitor for 380 ms at 18° eccentricity. The hue changed from 0° to 360° in steps of 17°, and the saturation was adjusted to the saturation acquired from the previous experimental procedure for 18° eccentricity. The observer had to respond whether the spot was red, blue, green or yellow. The whole procedure was repeated 20 times (for detailed description, see Parry et al., 2006). Four colour naming functions were obtained, one for each colour. Unique red, green, blue and yellow were defined as the central maxima of these function (for detailed description, see Parry et al., 2006).

Results

Experiment 1.
Asymmetric colour matching

Colour matching with 20° background, illuminant C compared with illuminant A

The results of matching are plotted in Lu'v' colour space (Figure 3a). It will be seen that an illuminant change from standard

C to test illuminant A is the most difficult compared with other test illuminants (S, G, R, V, Y) because the shift on the u'v' chromaticity plane is greater for this illuminant than for the others. This effect is clearly evident in Figure 2, see also J. J. Kulikowski et al., (2001). Consequently, the original colours of all the ten samples, (filled black diamonds) reflect medium-long wavelengths (filled black circles), under illuminant A and therefore would look orange-red on a black background (void vision, see stage 1 in Introduction).

Under these conditions, the presence of a background compensates for the physical shift, and the result of matching the different samples are shown by empty circles in Figure 3a.

Note that the neutral background under C is matched as indicated by a large empty circle M_C, and its apparent shift is indicated by a heavy dashed line which is about 45% of the physical shift from C to A. Thus, colour constancy is indicated by BR = 0.55. It will also be seen that the points marking matches shown by small empty circles (e.g. M_i) is shifted about the same distance from its corresponding (reference) points, (e.g. C_i). Thus, colour contrast depicted by the heavy lines between the original C_i to C and M_i to M_C is comparable (Figure 3a).

Figure 3b shows cone contrast for matches computed with respect to the perceived neutral background against the original cone contrasts of all ten samples under a test illuminant. It is evident that cone contrasts for matches correspond to the original, although colour constancy is poor. This effect is often referred to as 'discounting background', which is not quite appropriate since the background colour is not discounted (Colour plate 2).

Colour matching with 120° background illuminant C compared with illuminant A

The procedures are as in the experiment with 20° background, but the screen is viewed through a white cone-shaped tube providing a 120° surround. The adaptation time was first 1 s as before, then additionally extended to 60 s.

The results of matching are shown in Figure 4a by empty circles (1s) and empty diamonds (60 s); these points are all similarly shifted from the original filled diamonds. Thus, for 1-s presentation, matches are similarly shifted as for the 20° background. Colour constancy is about 50%, i. e. the match points are shifted on the average halfway between the reference and the test samples. A substantial improvement of colour constancy occurs for long (60 s) presentation times. Here, the empty diamonds almost coincide with the original filled diamonds. The background no longer looks orange after 60-s adaptation, which means that constancy is about 90%. Figure 4b illustrates the cone contrast for the matches under 1-s presentation time, and it is evident that they correspond well to the cone contrast under reference illuminant C (as in Figure 3b). The experiment shows that the cone contrast constancy rule is independent of colour constancy.

Colour matching of samples on 20° background under widely different illuminants

We have found conditions where the cone contrast rule is violated, namely when we chose the reference A (previously C) and a test illuminant S. Both these illuminants represent naturally occurring phases of daylight, illuminant A is morning sunlight

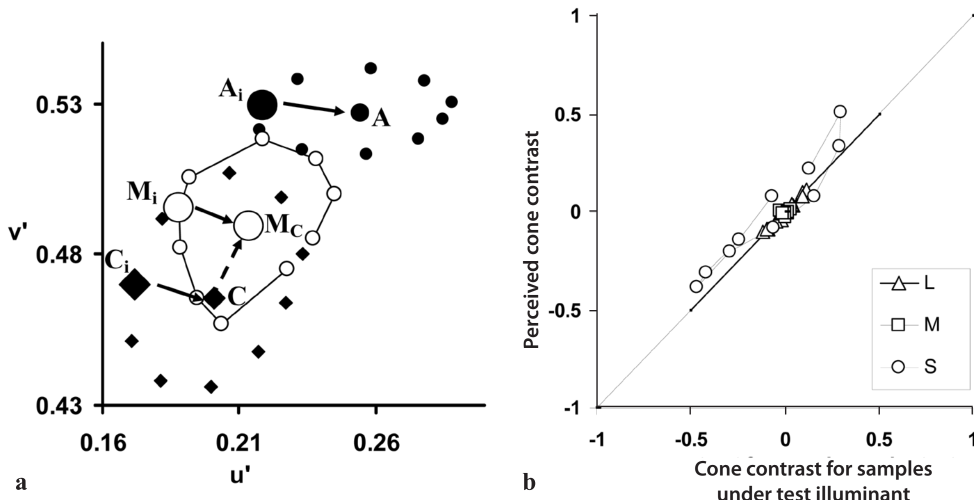


Figure 3.

(a) Locus of the 10 reference samples in u'v' space under illuminant C (filled diamonds). The test illuminant, in this case illuminant A, is depicted by filled circles. The corresponding matches are illustrated with empty circles. Example data for one subject using 1 s stimulus presentation and the 20° background. The locations of the test illuminant A are shown as a large filled circle. The reference illuminant (C) is a large filled diamond. M_C is the subject's perceived background under the test illuminant. Example points Ci and Ai indicate the physical location of an individual sample illuminated by C and A respectively. M_i indicates the matched location of the same sample when viewed under the test illuminant, in this case A.

(b) Perceived cone contrast (computed with respect to matched neutrality M_C) plotted against cone contrast under the test illuminant for the three cone types.

and illuminant S is northwest sky combined with snowfall. Figure 5 shows reference and matching ellipse in Lu'v' space and BR ≈ 0.5.

It is obvious that 'perceived neutrality' (M_A) is outside of the locus of colour matching for the samples. Consequently, the cone contrast rule does not hold for S-cones, as illustrated in Figure 5b.

Experiment 1. Summary

1) Matching of samples under different illuminations is ruled by their relative cone contrast, computed for matched samples against matched or perceived backgrounds. This cone contrast rule holds if illuminant changes are not excessive.
2) The rule is violated if the illuminant changes are substantial, even though changes are along those encountered in daylight.
3) Colour constancy is moderate, unless adaptation lasts minimum 1 min and a large neutral background is used.
4) Thus, bearing in mind that cone contrast constancy occurs almost universally and colour constancy varies from 0.4 to 0.9, we conclude that these processes are uncorrelated (Murray et al., 2006a, 2006b).

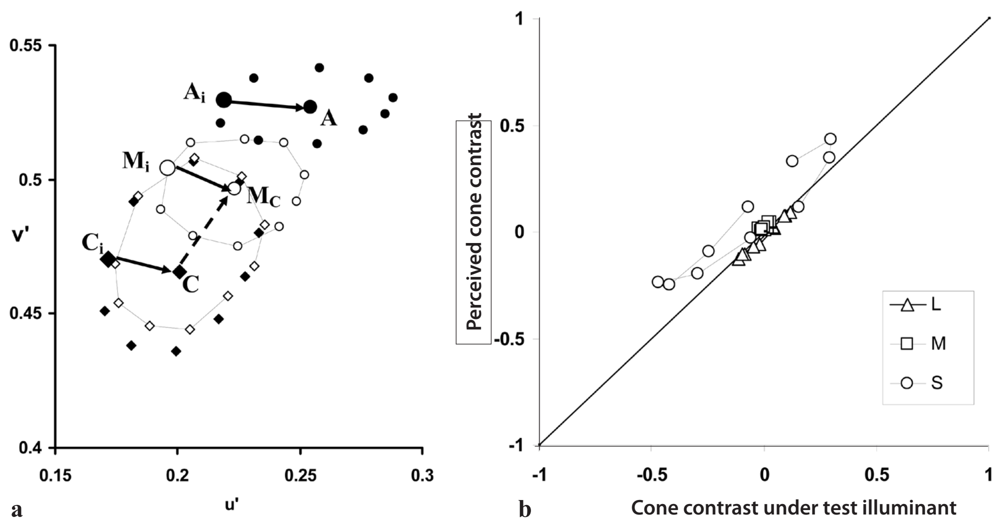


Figure 4.

(a) Perceived colour shifts induced by illuminant A for two adaptation durations and for a 120° field. Other details as in Figure 3, and the perceived shifts for 1 s presentation are similar to that for the 20° background (empty circles). The loci for the longest duration of 60 s (empty diamonds) show only a minimal shift away from illuminant C. Data are means of four subjects.

(b) Perceived cone contrast (as in Figure 3b) plotted against cone contrast under the test illuminant for the three cone types.

Experiment 2.
Peripheral colour matching

N. R. Parry et al. (2006) found that as the eccentricity changes, minimal hue distortion occurs for unique red (0° – cardinal red axis), blue (110°) and yellow (290°) but not for unique green (~200°). As discussed in their paper, the lack of correlation between peripherally invariant green (revealed by matching) and unique green may be linked to the wide ranges of green in natural scenes. Usually, unique red coincides with the cardinal L–M axis on the red side (0° axis in Figure 6) and with peripherally invariant red. In order to understand the link between peripherally-invariant and unique, it was necessary to find a subject for whom the unique red would be different from the cardinal red. Subject TP met this requirement as he has unique red at 17° on the chromatic axis.

Figure 6 shows the results of the peripheral asymmetric colour matching experiment. It is evident that, in accordance with N. R. Parry et al. (2006), saturation declines with eccentricity, mostly along the red–green cardinal axis (0°–180° axis). There is, however, a remarkable invariance of some hues. For example, in the red and green regions hues remain unchanged at virtually all eccentricities. Intermediate hues undergo quite extensive shifts (for details, see N. R. Parry et al (2006)). Unique red, blue, green and yellow are marked by filled stars for 1° eccentricity and by empty stars for 18° eccentricity. In the matching task, two peripherally invariant hues are at 195° in the green region and

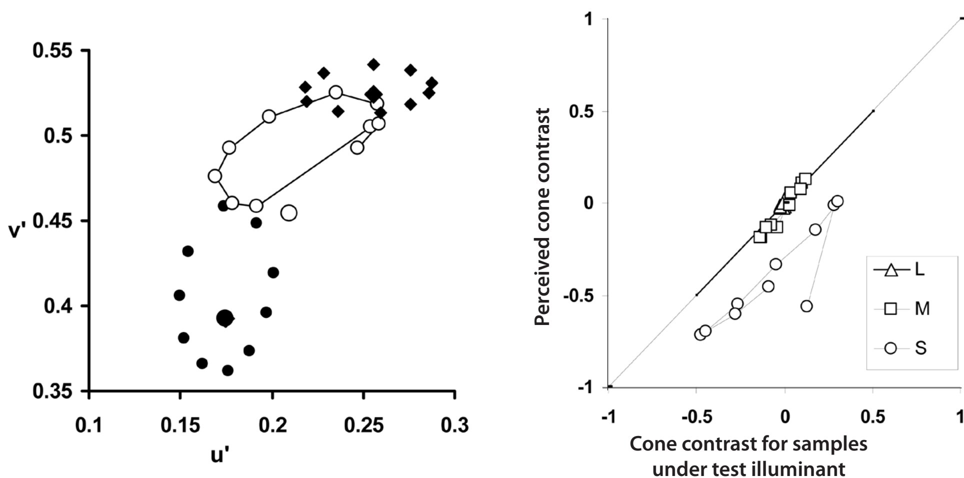


Figure 5.

(a) A case showing a breakdown of the cone-contrast rule. Filled diamonds describe the locus of the 10 samples taken as the reference under illuminant A (unlike in Figures 3 and 4 where C was a reference) with illuminant S as the test illuminant (filled circles). This double change in illumination (A to S – see Figure 2) makes the matching task difficult. Significantly, the perceived neutrality (large empty circle) is outside the locus of the matched samples (empty circles).
(b) Perceived cone contrast (computed with respect to matched neutrality) plotted against cone contrast under the test illuminant. In this case, the von Kries law is violated.

at 17°. Note that the peripherally invariant green (195°) is considerably different from unique green (~225°). This is puzzling since unique green was the same (225°) for both eccentricities (see below). At the red region, the invariant hues in the matching task are close to unique red (17°). Thus, peripheral colour matching reveals hue shifts towards the L–M axis only for green. Other non-invariant hues tend also to converge towards the cardinal M–L axis; note that the dashed lines in the yellow-green region are rotated anticlockwise and those in blue-green clockwise, indicating some bias towards cardinal green.

On the other hand, when unique green is determined by the method of forced-choice, it is the same for both eccentricities, as indicated by filled stars and empty stars, respectively (Figure 6). Evidently, colour matching, which includes hue, saturation and brightness combined, is biased towards maximum saturation changes. This may mean a stronger contribution of cone-opponency in this region of high sensitivity.

Discussion

What makes colour samples appear matched?

Although colour matching involves combined matching of hue, saturation and brightness, the exact weighting of these parameters in not known. We can have some insight from some special cases; e.g. in experiment 2 unique green at the periphery does not match unique green

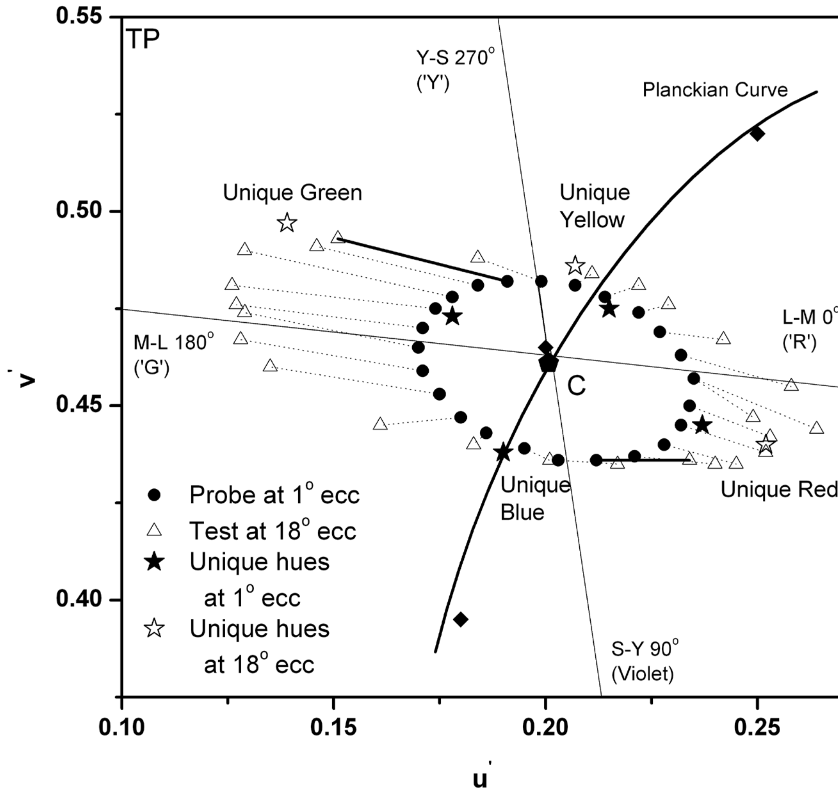


Figure 6.

Colour matching data plotted in CIE1976 u'v' colour space. Two axes, named L–M and S–(L+M), are the two cardinal axes ('Red-Green' and 'Blue-Yellow' respectively). Black filled circles depict the chromatic loci of the 1° reference spot at 1° eccentricity. The empty triangles represent the colour matches of the 3° test spot, for subject TP, at 18° eccentricity (nasal field). Each reference data point is connected by a dotted line with the analogous matched point. Two solid lines which connect two reference points with two matched points show the two maximum hue rotations. Stars show the unique hues for 1° (filled stars) and 18° (empty stars). The Planckian curve is the locus of the daylight variations. Note that unique hues at both eccentricities are similar when obtained by forced choice (see Methods), but the colour match of unique green is rotated towards the cardinal 'G'.

viewed para-centrally. Obviously hue similarity is outweighed here by matching the other parameters. The most important observation from the experiments presented here is that no single transformation can explain how colours are perceived when matched. A similar conclusion was reached by J. M. Kraft, D. H. Brainard (1999) and many others, but some studies used more complex (natural) stimuli. Here, the visual stimuli have a simple spatial arrangement (chromatic patches) on a neutral background. The two tasks presented here, colour matching of differently illuminated samples and colour matching of differently located samples, look very similar. However, the outcome is very different in both these cases. The

first task is done according to the perceived cone contrast between the samples and a neutral background (cone-opponent stage), whereas the latter demonstrates the constancy of unique (or categorical) hues, which may be determined by a higher stage of colour opponency.

Such differences in contributions of different mechanisms are seen in other tasks, e.g. in detection and discrimination. The spectral sensitivity of chromatic samples on neutral background can be fitted by two cone-opponent functions, the L–M and the S–(L+M) cone-opponent mechanisms (King-Smith and Carden, 1976; Kranda and King-Smith, 1979). However, a reliable discrimination of hues at their detection thresholds occurs when these spectral samples cross categorical borders, which means that this is possible only between unique (categorical) hues (Mullen and Kulikowski 1990). Thus, the colour opponency (3rd stage of colour processing) determines hue discrimination for central and peripheral viewing (Figure 6). In our case, unique hues also serve as markers for the organization of colour vision across the visual field, adapted specially to daylight conditions.

The proximity of invariant hues to unique blue, red and yellow and to the Planckian curve may not be coincidental since the unique hues are essential for natural daylight perception. Only the unique green is distant from the Planckian curve. Informal measurements in an Australian tropical forest park showed a very little departure from the daylight curve towards green, as though reflections from the green canopy had no significant contribution to illumination.

Strategies of colour matching under different illumination: limits of cone-contrast rule

Over a hundred years ago, von Kries established that colour samples under different illumination are matched if they have the same colour contrast components which are signalled by the three cone contrast mechanisms and served by the cone-opponent mechanisms (2nd stage, retina). This cone contrast rule was later revised and qualified in various studies (Arend and Reeves, 1986; Shevell, 1978; Nascimento and Foster 1997; for review, see Whittle, 2003). A series of our studies (Murray et al., 2005; Stanikunas et al., 2005; Daugirdiene et al., 2006; Murray et al., 2006a, 2006b) reasserted that the cone-contrast rule holds if contrast is computed between perceived colours and perceived neutral background. A tacit assumption was that the illuminant's shifts do not exceed the doubled shift of a Munsell chroma level of 4, as illustrated in Figure 2 for a change from the standard illuminant C to the test illuminant A. This change, from C to A, occurs during the day, e.g. when the sun is covered by clouds and then later in the evening reappears, giving orange illumination. A is also associated by the tungsten bulb. Although such condition occurs naturally, it is in fact a greater change than for other illuminants (Figure 2) and thus it was chosen as the most difficult test. In the original papers, we tested the cone-contrast rule with 6 illuminants and four different paradigms. In all these cases, the cone-contrast rule held (Daugirgiene et al., 2006). However, the situation where illuminant A was chosen as reference and S as the test proved to be over the limit for the viability of the cone-contrast rule (Fig.5b).

Cone-contrast rule is not directly related to veridical colour constancy

However, in spite of nearly universal validity, it is possible to have poor colour constancy when the cone contrast rule holds (Daugirdiene et al., 2006, Murray et al., 2006a, 2006b). Colour constancy improves substantially only when the background covers a large part of the visual field and adaptation lasts at least 1 min, whereas the cone contrast rule applies in all these cases. In other words, the cone contrast rule does not help in finding real colours, as shoppers know when trying to find real daylight. As we can see from a simple demonstration (Plate 2), under certain conditions illumination is not discounted, and colours depart substantially from those seen in the daylight. Thus, viewing of a restricted part of a scene, like through a keyhole, never achieves colour constancy. It may go halfway as illustrated in Figure 4, but will not improve with adaptation time (Murray et al., 2006a). It seems that cone-opponency is a fast mechanism which judges whether objects within a scene change, or whether illumination changes (Foster and Nascimento, 1994), rather than estimating true colours. It is important to recognize that these two mechanisms should be regarded as different, otherwise the cone contrast rule would become synonymous with colour constancy of retinal origin, and this is incorrect.

Large visual field and long viewing improve colour constancy

Improvement of colour constancy requires both enlargement of the visual field and a long adaptation time (Figure 4). Observation under 120° background and 1-s presentation time shift all the colours like the 20° visual field. But white seems really white after a1-minute viewing of a large scene, although a good observer still notices the difference.

Cone-opponency versus colour opponency

It seems that in most conditions cone-opponency solely determines colour matches. This is puzzling since some contribution of colour-opponency and unique hues might be expected. Some colour vision models explicitly incorporate the 3rd stage (Nakano et al., 1988; De Valois et al., 1997). J. J. Kulikowski, H. Vaitkevicius (1997) specifically examined whether colour constancy was significantly better for unique hues, using real Munsell samples (value 7, chroma 6) and pre-testing the subjects on unique hues. The constancy index (BR) was slightly higher for unique hues but did not reach statistical significance. For other conditions, especially with display-simulated Munsell samples, there was no better constancy for unique hues. Moreover, the effect of brightness on related colours (brown, beige, khaki and dull-blue) can also be explained by a cone-opponent model (Stanikunas et al., 2005). This is consistent with the notion that cone-opponency is the main process determining colour matching in variable illumination. It is rather surprising that colour matching based on the cone-contrast rule operates over so many conditions and that so little influence (if any) of the colour-opponent stage and unique hues is observed (Kulikowski and Vaitkevicius, 1997). Conversely, peripheral colour matching reveals the prominence of unique blue, red and yellow; these hues correspond to those which do not undergo

a shift in the periphery. Evidently, colour matching in this task is determined mainly by the processes that determine the invariance of unique hues. For reasons not yet totally understood, unique green does not correspond to peripherally invariant green. Here, colour matching seems biased towards cardinal green, as if cone-opponency, rather than higher stages, dominates green in the periphery (see Figure 6 and Parry et al., 2006). Given that matching experiments are usually driven by cone-opponent mechanisms, it is perhaps surprising to find that three out of the four unique hues correspond with the peripherally invariant hues.

Balance between sensitivity and selectivity

As mentioned before, chromatic detection is served by highly sensitive cone-opponent mechanisms, whereas wavelength discrimination mechanisms are selective to unique hues (Mullen and Kulikowski, 1990; Stoughton and Conway, 2008). However, selective trigger feature neurons in the visual cortex may not be the only mechanism to account for unique hues and their significance.

Over the past years, several similar problems have been explained in terms of the contribution of cell assemblies rather than highly selective trigger feature detectors. Examples are 'hyper-acuity' – seeing the fine lines – and stereo-acuity, both involving angular sizes 0.2 min of arc, i.e. beyond the resolution limit of foveal cones. In fact, the detection of fine lines was shown to be mediated by assemblies of most sensitive neurons (Kulikowski, 1967; Kulikowski and King-Smith, 1973; King-Smith and Kulikowski, 1980) and not by fine line detectors. Likewise, stereo-acuity has been modelled (Vaitkevicius et al., 1984; Lehky and Sejnowski, 1991) based on many neurons acting in unison. In particular, a minimum of 17 visual cortical neurons are sufficient, but crucial to the stereo-limit is the contribution of units with the steepest portions of the 'near-far' curves and not of units with the narrowest tuning curves (Lehky and Sejnowski, 1991). This is the theory of 'distributed representations'.

Possible neural basis and general mechanisms

Cone-opponency originates in the retina and is a relatively simple process. As postulated and quantified, cone-opponency is the 2nd processing stage, followed by the 3rd colour-opponent stage extracting unique hues (Wyszecki and Stiles, 1982).

The precise origin of this 3rd stage is still unknown (see Introduction). This process must certainly originate from relatively early stages since lesions in extra-striate cortical areas do not abolish perception of unique hues (Walsh et al., 1992). Although clusters of cells tuned to unique hues are found in higher visual cortical areas (Temporal) – TEO/IT, they might originate in earlier stages. There are many parallel projections from V1/V2 to TEO and IT areas to account for this. Many chromatic sensitive cone-opponent cells (arranged along the cardinal axes) were recorded in LGN (Derrington et al., 1984), but they have poor selectivity and their involvement in processing veridical colour has been questioned (Calkins, 2004). J. J. Kulikowski et al. (1997) have noted how difficult it is to separate the colour stream from the rest of chromatic processing, although it seem

to be a separate mechanism (Kulikowski and Walsh, 1995). In the primary visual area, V1, many cells receive dual inputs from the LGN: parvo- and konio-cellular (whose signatures are cone-opponency: L-M and S-L-M) and magnocellular which are now unanimously considered as the basis of luminance-contrast processing. T. R. Vidyasagar et al. (2002) found that the dual–input cells have a high contrast sensitivity, thus they are prime candidates for contribution to cone-opponent processing. Consistent with this notion of V1 being essential to cone opponency and hue processing are three findings: (1) cone contrast information is processed dichoptically, which suggests cortical computations (Nascimento and Foster, 2001); (2) necessity of using luminance reduction of a reference sample in order to match the isoluminant test sample/background – the 'dimming effect' (Kulikowski et al., 2001; Murray et al., 2005). The subjects in these cases need to reduce luminance in order to be able to match certain colours (appearing brown, beige, khaki and dull-blue). V1 is the first stage in which inputs from both eyes and both parvo/konio (cone opponent) and magno (luminance) signals are combined; (3) the role of V1 was identified in a patient with a V1 lesion. This is a case of residual vision ('blind-sight') in the left hemi-field. The patient's residual colour vision relied only on wavelength information (Kendridge et al., 2007). Hence, we can conclude that V1 must be necessary to the transmission of both cone-opponent and hue signals.

It is possible that the cells involved in signalling unique hues are selective enough to serve hue discrimination, but not sensitive enough to determine colour matching tasks, when competing with cone-opponent units (see 'unique green' in Figure 6). Since many chromatic sensitive cells have a poor colour selectivity, two separate processing streams have been postulated, one specializing for colour and the other for chromatic pattern–texture–stereo and motion (Kulikowskia and Walsh, 1995; Kulikowski et al., 1997; Calkins, 2004). The colour stream may originate in some colour selective retinal/LGN cells, but the chromatic stream contains (in V1) some cells with dual parvo/konio-magno inputs which increase their contrast sensitivity (Vidyasagar et al., 2002). The visual cortex could build up the integrity of colour vision across the visual field based on the invariant hues that are related to natural illumination. Three out of four invariant hues are the unique hues that are associated with daylight illumination changes (blue, red, yellow). Unique green is not associated with daylight, and thus different adaptation may lead to variability (Jordan and Mollon, 1997) making it additionally difficult to be established as invariant in colour matching tasks. Another possibility is that unique hues are connected with the minimum noise in the system (Kulikowski, 2003), but testing this idea would require a specific series of experiments. Nonetheless, both cone-opponent and unique hue signals are likely to result from responses of many cells, as suggested by the unreliability of single-neuron signals.

Final stages: V4 and beyond

The primary visual cortex (V1) is a major relay centre which packages various attributes of a visual scene, such as spatial frequency, orientation and colour, and sends many parallel projections to other

visual areas (Zeki, 1983, 1993). The pathway processing colour information is concentrated in occipital and temporal areas. Localized brain lesions may not cause as severe damage to colour perception as in the early processing stages, but they may be quite informative about normal brain function. Selective damage to visual cortical area V4 (Zeki, 1983) does not affect hue discrimination and the use of unique hues (Walsh et al., 1992, 1993) in perceptual tasks, but persistently impairs colour constancy (Wild et al., 1985; Carden et al., 1992; Zeki et al., 1999). It seems that V4 complex is a centre of expertise providing highly specialized information about colour (Zeki et al., 1998). Its lesions abolish this expertise, but do not impede the basic colour processing.

This is in stark contrast to the effects of retinal-optic nerve lesions, which are well localized and predictable. Damage to the parvo/konio systems abolishes colour vision (King-Smith and Kulikowski, 1980). Only if cortical lesions are extensive, affecting several consecutive areas, then colour signals may be severely affected, resulting in severe achromatopsia. Commonly, however, we observe partial colour vision deficiencies, or various kinds of dyschromatopsia.

Concluding remarks

1. Colour samples under different illumination are commonly matched according to their cone contrasts unless illuminant changes are excessive. However, matched colours depart from the colours seen in daylight, especially under restricted viewing conditions. Poor colour constancy does not necessarily rule out the applicability of the von Kries law. We show conditions (e.g. keyhole viewing, see above) where colour constancy is poor when the von Kries law holds.
2. Increasing the visual field size from 20° to 120° in a matching experiment facilitates high values of colour constancy, but only for viewing times of 60 s and above. This implies that the colour apparatus uses signals derived from the entire visual field (i.e. panoramic viewing), perhaps using some form of spatial and temporal integration. This observation is supported by the fact that when a matching paradigm is used to compare peripheral and central colour samples, the peripherally invariant hues correspond to unique hues. This in turn suggests that veridical colour perception is based on integration across colour space, relying on the chromatic anchor points at red, blue, green and yellow, rather than on simply spatio-temporal integration. It is crucial to recognize that the phases of daylight, ranging as they do between red, yellow and blue, must have played a major role in the evolution of stable colour perception.
3. Finally, there is a trade-off between sensitivity and selectivity, and it seems likely that neurons form flexible assemblies which can act together to extract either hue, giving a fine hue discrimination but a poor sensitivity, or extract contrast giving a high chromatic sensitivity but having a poor hue discrimination.

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INFORMACIJOS APIE SPALVĄ APDOROJIMO SMEGENYSE STADIJOS

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S a n t r a u k a

Spalvinės informacijos apdorojimas regos sistemoje pereina keletą stadijų. Primatų spalvinė rega priklauso nuo trijų fotoreceptorių, kūgelių, kurie tiria matomą šviesą ir siunčia signalus kitai, oponentinių ląstelių stadijai. Šioje stadijoje nustatomi chromatiniai slenksčiai ir atliekamas paviršiaus spalvų suvienodinimas keičiantis apšvietai. Sugebėjimas skirti spalvinį toną absoliutaus slenksčio lygiu atskleidžia trečią, spalvų oponentiškumo, stadiją, kurioje apibūdinamos spalvų kategorijos, dar vadinamos unikaliomis spalvomis. Ši stadija jau reikalauja indėlio iš smegeninių spalvos analizės centrų (V4-komplekso, temporalinės-okcipitalinės žievės).

Šio darbo tikslas: pristatyti pagrindinius eksperimentus, iliustruojančius oponentinių ląstelių ir unikalių spalvų indėlį į pirminį spalvinės regos lygį (pirma ir antra stadijos), ir aptarti, kokią įtaką visai regos sistemos struktūrai turės atskirų spalvos apdorojimo stadijų pažeidimas.

Buvo atlikti dviejų tipų eksperimentai:

- Asimetrinis spalvų sulyginimas, kai pateikiamas 2° stimulas centrinėje regos dalyje, apsuptas 20° arba 120° foninės aplinkos.
- Spalvų sulyginimas centrinėje ir periferinėje regos lauko dalyje, nutolusioje 18° nuo centrinės dalies.

Nustatyta, kad padidinant regimąjį lauką nuo 20° iki 120° ir adaptacijos laikui esant ne trumpesniam kaip 60 s, labai pagerėja spalvų konstantiškumas. O tai reiškia, kad spalvoms suvokti reikia informacijos iš viso regos lauko (panoraminė rega), ir šiai informacijai rinkti naudojamas tiek erdvinis, tiek laikinis integravimas. Panoraminės spalvinės informacijos apdorojimo hipotezę patvirtina ir tas faktas, kad, atliekant spalvų sulyginimą centrinėje ir periferinėje regos lauko dalyje, stabilios periferinės spalvos sutampa su unikaliomis spalvomis. Taigi, tikrasis spalvų suvokimas nebus vien paprastas receptorių signalų integravimas erdvėje ir laike, bet greičiau remsis keturiomis bazinėmis spalvomis ir jų maišymu visoje spalvų erdvėje. Be kita ko, dar turėtų būti tam tikra neuronų jautrumo ir selektyvumo spalvoms pusiausvyra. Todėl tikėtina, kad susiformuoja prisitaikantys neuroniniai ansambliai, kurie gali tiksliai nustatyti absoliučią spalvą ir turi mažą jautrumą spalvos skirtumams, arba gali tiksliai nustatyti spalvos skirtumą, bet tada apytiksliai nustatoma absoliuti spalva.

Pagrindiniai žodžiai: spalvų konstantiškumas, spalvų sulyginimas, kūgelių kontrastas, unikalios spalvos, paskirstytoji struktūra.

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