



# Multi-coloured stereograms unveil two binocular colour mechanisms in human vision

Casper J. Erkelens<sup>\*</sup>, Raymond van Ee

<sup>a</sup> *Helmholtz Institute, Utrecht University, P.O. Box 80.000, 3508 TA Utrecht, The Netherlands*

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## Abstract

Two different colours, one presented to one eye and the other presented to the other eye, often create the impression of a third colour. This percept is known as binocular colour mixture. Here we use coloured stereograms to study binocular colour appearance. Vivid pastel colours are induced in monocular, achromatic patches, if these are placed in stereograms whose left and right images differ in colour. The build-up of the colours is slow and takes tens of seconds or even minutes in certain individuals. The induced colours remain visible during monocular viewing of the patch and decay gradually. The same colours are induced irrespective of whether the patches are placed in fusible or rivalrous stereograms. We show that these colour effects cannot be induced by monocular colour mechanisms, either alone or in combination with binocular colour mixing. We suggest that the colours are induced by a binocular feedback mechanism, which reduces colour differences between the colour appearances of two monocular images. Induced colours are not observed if the achromatic patches are binocular. However, induced colours are apparent if one switches to monocular viewing after prolonged binocular viewing of the binocular patches. This aftereffect suggests that binocular colour induction acts on the monocular representations of binocular images. We suggest that during binocular viewing the fast process of binocular colour mixing masks the changes in colour appearance produced by the much slower process of binocular colour induction. © 2002 Elsevier Science Ltd. All rights reserved.

*Keywords:* Binocular vision; Colour perception

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## 1. Introduction

When we view a stereogram whose left and right images are of different, but uniform, colours, we perceive a stereoscopic image whose colour differs from the colour of either image. This property is explained by the theory of binocular colour mixing (Hering, 1879/1942). Binocular mixing of different colours has been a controversial issue for nearly two centuries (Hovis, 1989): there are those who question its occurrence (Dunlap, 1944; Haldat, 1806; Helmholtz, 1910/2000; Hurvich & Jameson, 1951) and those who believe in its occurrence (Dawson, 1915; de Weert & Levelt, 1976; Gunter, 1951; Hecht, 1928; Hering, 1879/1942; Hoffman, 1962; Hovis & Guth, 1989; Howard & Rogers, 1995; Humanski & Shevell, 1985; Ikeda & Nakashima, 1980; Ikeda & Sagawa, 1979; Johannsen, 1930; Lange-Malecki, Creutzfeldt, & Hinse, 1985; Prentice, 1948; Sagawa, 1982;

Thomas, Dimmick, & Luria, 1961; Trendelenburg, 1923), but disagree about the necessary conditions (Howard & Rogers, 1995). Many researchers hold Hering's (1879/1942) view that binocular colour mixing explains binocularly perceived colour although no quantitative theories exist so far.

The colours of objects can differ in the two eyes because of slightly different positions of the light source relative to the eyes. Anaglyphs generate very special colour differences in that they are extreme and uniform throughout the visual field. Apparently, the visual system of most individuals can find a solution even for such unnatural colour differences. Induced colours arise slowly in monocular patches of binocular fused anaglyphs, if their colours differ from those of the images in which they are placed. Fig. 1 shows three examples of white patches placed in anaglyphs containing different colour combinations (Fig. 1a). It may take minutes before the colours become vivid. Informal evaluation of the colours by dozens of subjects indicated that the strength of the effects strongly depends on the

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<sup>\*</sup> Corresponding author. Fax: +31-30-2522664.

*E-mail address:* c.j.erkelens@phys.uu.nl (C.J. Erkelens).

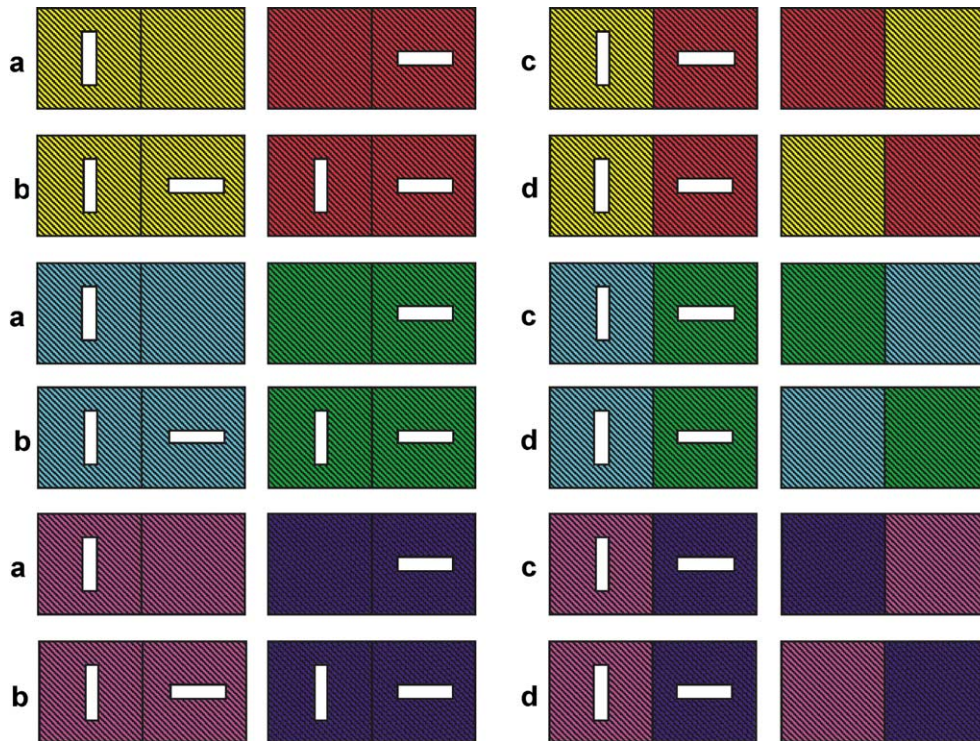


Fig. 1. Binocular colour induction in monocular patches. Sets of four multi-coloured stereograms are shown for three different colour combinations. (a) The white, monocular patches gradually fill with distinct pastel colours during binocular viewing of the stereograms. The build-up of the effect typically takes a few seconds. Dependent on the viewer, the full development of the colours may even take minutes. The colour effects are most compelling when the stereograms are viewed in bright light. When one eye is closed the illusion gradually becomes weaker and disappears. This build-up and decay of the illusion after opening or closing one eye indicates that the colour appearances are induced by a binocular mechanism. (b) During binocular viewing, the white, binocular patches do not change colour. During monocular viewing after a period of binocular viewing, however, induced colours are apparent in the patches. (c) Locally, the colours surrounding the patches are the same as the colours shown in (a). In contrast to the induced colours of (a), colours are hardly apparent in these patches. (d) Locally, the colours surrounding the patches are the same in both eyes' images. Colours are hardly induced in the patches. The absence of colour effects in the patches of (c) and (d) demonstrates that binocular colour mixing does occur in rivalrous patches. It also shows that binocular colour induction is not explained by local colour contrast in combination with binocular colour mixing.

combination of background colours, the eye viewing the patch and the viewer. Induced colours are fully absent if the fused anaglyphs contain binocular white patches (Fig. 1b). The patches remain white even after prolonged binocular viewing. However, the constant whiteness of the patches is deceptive because it masks the ongoing process of colour induction. If one rotates the head leftwards or rightwards so that fusion breaks, one can immediately see the induced colours in the now monocular patches.

Monocular mechanisms affect colour signals before binocular integration takes place (Chichilnisky & Wandell, 1995; Rinner & Gegenfurtner, 2000; Shevell, 1978; Walraven, 1976). Hence a demonstration of binocular colour processing must rule out the possibility that colour appearances result from monocular mechanisms. Prolonged monocular viewing of any of the images of Fig. 1a and b demonstrates that colours induced in the patches are faint and different from those experienced during binocular viewing. From this demonstration it is clear that monocular mechanisms alone

cannot explain the binocular colour appearances of the monocular patches.

A binocular explanation for the effects is that the colours are induced by monocular colour contrast of the patch relative to its surround in combination with binocular colour mixing between the patch and the colour of the other eye's image. Fig. 1c and d demonstrates that binocular colour mixing does not occur in these images. In Fig. 1c, the colours that are assumed to mix are the same as those presented in Fig. 1a. However, colours are hardly induced in the patches of Fig. 1c. In fact, the faint induced colours are very similar to those of the patches shown in Fig. 1d although the colours that are assumed to mix are very different.

It is evident that binocular colour mixing cannot explain the colour appearances of the monocular patches. We are forced to conclude that the colours result from a binocular mechanism that is different from binocular colour mixing. In this study we investigate how colour appearances of monocular patches are affected by the colours of their surrounds in both eyes' images.

## 2. Methods

### 2.1. Subjects

Ten subjects participated in the experiments (ages between 24 and 50 years). None of them showed any visual or oculomotor pathologies other than refraction anomalies. The subjects had normal or corrected-to-normal visual acuity. They were checked for normal colour vision by means of the Ishihara colour test. Two of the subjects were not able to mix the colours of red/green anaglyphic stereograms, although they perceived the hidden figures in depth. We included the results of these subjects in our analysis because their colour induction was indistinguishable from that of the other subjects.

### 2.2. Stimuli and analysis

Stimuli were displayed on a colour CRT monitor (LaCie) in an otherwise dark room. A spectroradiometer (SpectralScan 704) was used to measure the spectra of the red, green and blue phosphors at their maximum intensity setting. The spectra were multiplied by the CIE 1931 chromaticity functions, as revised by Judd (1951) and Vos (1978) to derive CIE  $x$ ,  $y$  chromaticity co-ordinates of the phosphors. The primaries of our monitor had chromaticity co-ordinates of 0.62, 0.34 (red), 0.27, 0.61 (green) and 0.15, 0.08 (blue). All stimuli were presented at an intensity that was normalised to the maximum intensity of the primaries.

Stereograms were presented that consisted of two differently coloured rectangular surfaces ( $10^\circ \times 6^\circ$ ). The surfaces were displayed in red, yellow, green, cyan, blue or magenta and contained grey monocular patches (see Fig. 2). The surfaces were dichoptically viewed at a distance of 57 cm by means of a stereoscope. A stereoscopic pair of  $xy$ -chromaticity diagrams ( $6^\circ \times 6^\circ$ ) was presented  $2^\circ$  above the two surfaces. The diagrams were coloured by colours representing the chromaticity values. Co-ordinate axes were drawn around the diagrams, which enabled the subjects to indicate the chromaticity values with a precision of 0.01. Ten observers viewed the 15 possible combinations of the differently coloured surfaces, which were presented in a random order. Each combination was presented three times with different types of monocular backgrounds (see Fig. 2): (1) fusible images in combination with rivalrous patches (Fig. 2a), (2) rivalrous images (Fig. 2b), and (3) fusible images that contained half-occlusions (Fig. 2c). The latter stimulus was added to demonstrate that the colour effects also occur during the viewing of stereograms that represent realistic objects.

After viewing the stereograms for at least one minute, the observers were asked to indicate the chro-

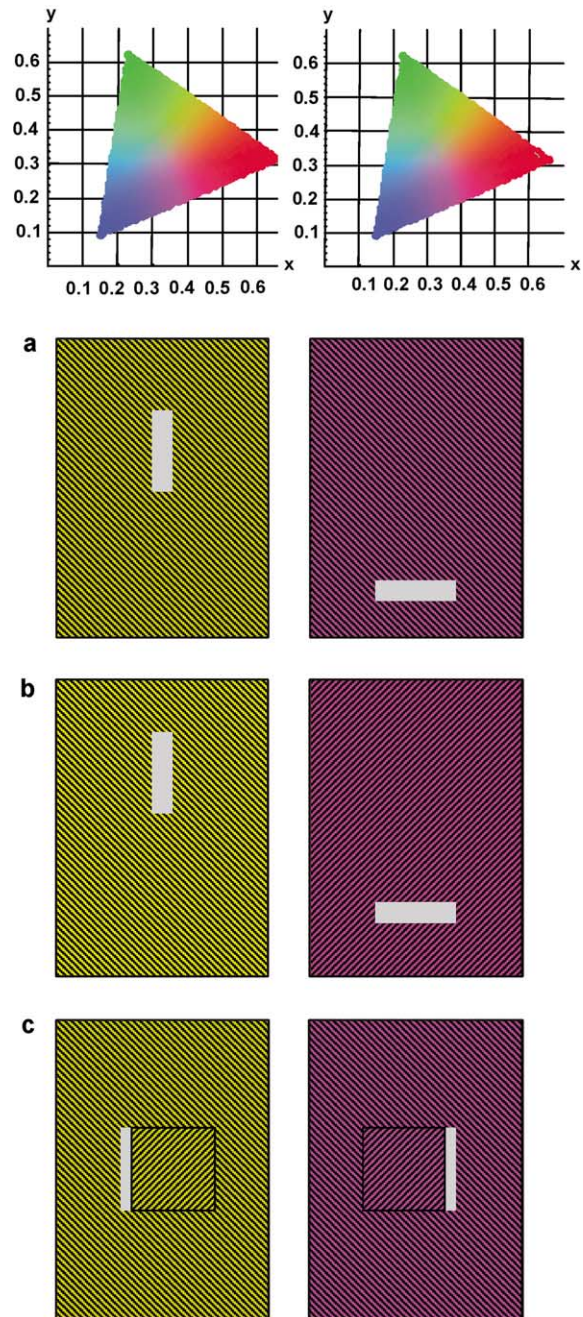


Fig. 2. Stimuli used in the binocular colour matching experiment. In each trial, one of the three stereograms (a, b, c) was presented in combination with the binocular chromaticity diagram. Stereogram (a) depicts a rectangle which contains two rivalrous, achromatic patches placed on a fusible pattern. Stereogram (b) depicts a rectangle which contains the same patches placed on a rivalrous pattern. Stereogram (c) depicts a completely fusible image. During binocular viewing colours arise in the patches. The patches in the yellow images become purple and those in the magenta images become green.

maticity co-ordinates of the colours that best matched the illusory colours of the two binocularly perceived monocular patches. For all statistics,  $t$ -tests were applied.

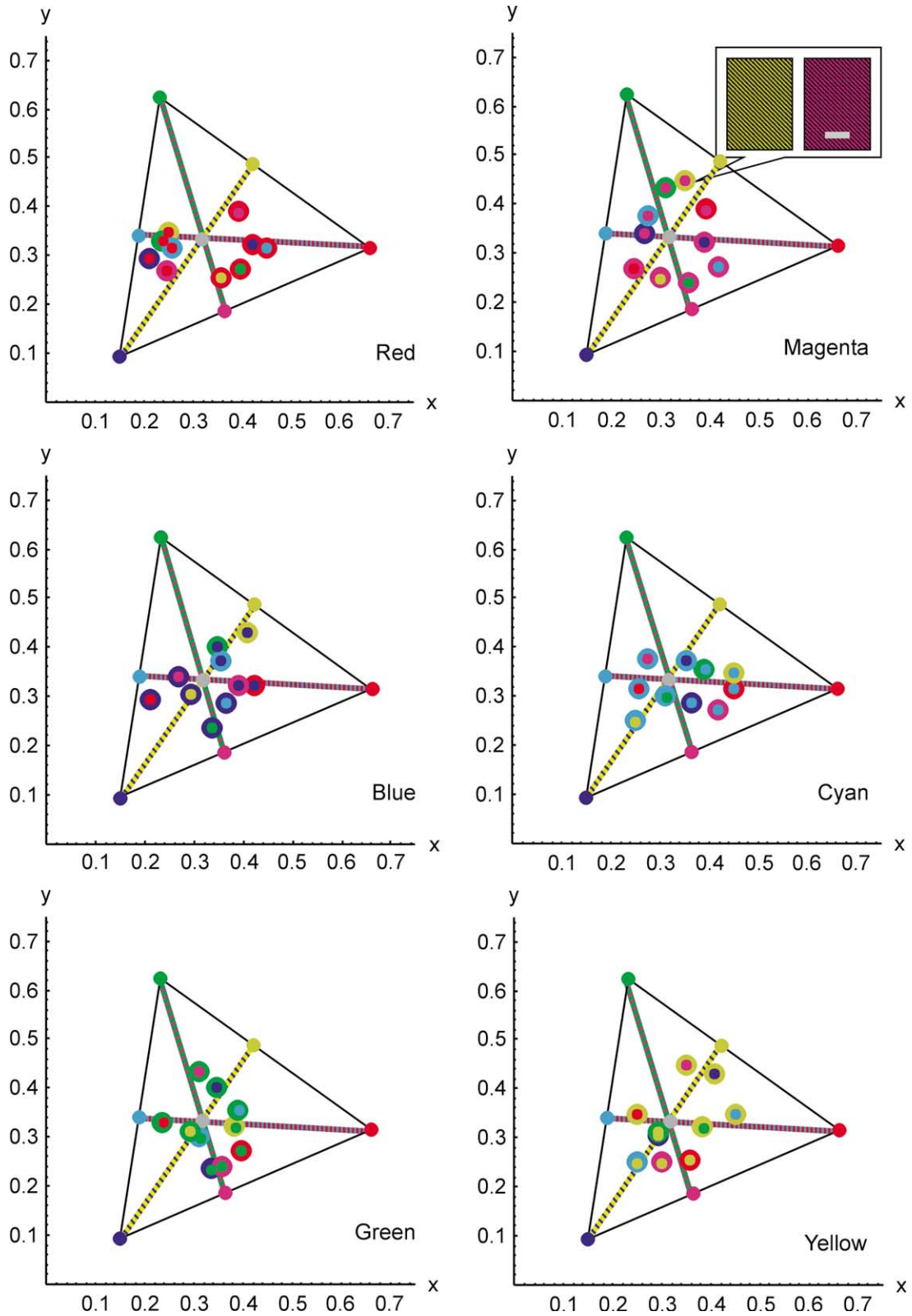


Fig. 3. Binocular colour matches. Mean settings are presented in six  $xy$ -chromaticity diagrams, one diagram for each image colour. The colours used in the experiments are indicated by solid dots. The chromaticity value of the monocular patches is indicated by the grey dots. The bi-coloured lines connect opponent image colours. The gamut of the monitor is indicated by the triangles. The bi-coloured disks represent mean values across subjects. Each disk consists of a centre of one colour surrounded by a surround of another colour. The centre indicates the colour of the image in which the patch is placed; the surround indicates the colour of the other image (see inset).

### 3. Results

Ten subjects matched the colour of each monocular patch to one of the colours of the  $xy$ -chromaticity diagram by estimating its co-ordinate in the diagram. All subjects experienced induced colours including the two subjects who were not able to experience a mixed colour in anaglyphic stereograms. There were objective and subjective differences between the matches of individual subjects. Four subjects showed strong asymmetries between the settings, depending on whether the left or the right eye viewed the patches. They experienced strong induced colours in one eye whereas these colours were almost absent in the other eye. Two subjects experienced the colours as very unsaturated in both eyes, whereas four subjects judged the colours as vivid and deep. Fig. 3 shows mean judgements across the 10 subjects, the three types of stimuli and the two eyes. Standard deviations are about the size of the symbols. The location of each mean value is significantly different ( $p < 0.01$ ) from that of the grey dot. In each panel the mean values appear to be grouped in a characteristic way, which indicates that the colours of both images affect the colours of the patches. All symbols having coloured dots of one colour (for instance the magenta dots in the “magenta” panel) are shifted towards the opponent colour (green). All symbols carrying rings of one colour (the magenta rings in the “magenta” panel) are shifted to their own colour (magenta). The distribution of mean values indicates that the two images affect the colours of the patches in different ways. Apparently, the mechanism responsible for the induced colours pulls the colour appearance towards the colour of the other eye’s image and pushes it away from the colour of the image in which the patch is placed.

We divided the matches of the subjects into three groups related to the type of stereogram in which the patches were placed (see Fig. 2). Statistical analysis of the matches showed no significant ( $p > 0.05$ ,  $t$ -test) differences between the three groups of matches. This result indicates that the colours are induced by a mechanism that operates independent of stereopsis.

### 4. Discussion

#### 4.1. Mechanisms of binocular colour processing

We present novel colour effects in multi-coloured stereograms. The demonstrations of Fig. 1 show clearly that the effects are induced by a binocular colour mechanism. We call the mechanism “binocular colour induction” to distinguish it from binocular colour mixing.

#### 4.2. Conditions for binocular colour mixing and induction

The optimal conditions for binocular colour mixing seem very different from those for binocular colour in-

Table 1  
Optimal conditions for binocular colour processes

Conditions	Binocular colour mixing	Binocular colour induction
Image		
Brightness	Dim	Bright
Size	Small	Large
Colour	Desaturated	Saturated
Wavelength	Not far apart	Far apart
Stereopsis	Required	Not required
Representation	Binocular	Monocular
Dynamics	Fast	Slow

duction (Table 1). According to the literature, binocular colour mixing occurs only under the following restricted conditions: (1) binocular stimuli are equal in size and smaller than  $1^\circ$ ; (2) the surround is dark; (3) colours are desaturated, dim, and equal in brightness; (4) wavelengths are not far apart; and (5) the amount of fusional vergence required by the subjects is minimal (Hovis, 1989; Johannsen, 1930). Our demonstrations suggest that the optimal stimulus conditions for binocular colour induction are just opposite to these conditions. The induced colours become really vivid when the stereogram is bright, its size is large, the colours are saturated and the wavelengths of the two images are far apart.

The patches shown in Fig. 1c and d do not mix with the colours of the other image. This example suggests that binocular colour mixing does not occur between rivalrous images. The example of Fig. 4a demonstrates that binocular colour mixing depends on stereoscopic processing. The stereogram of Fig. 4a contains two squares, whose colours are green in one image and red in the other image. The locations of the squares are shifted horizontally so that, in binocular viewing, one square is lying behind and the other in front of the grey surround. In binocular viewing we perceive yellowish squares if binocular colour mixing is successful and alternating red and green squares if it is not, irrespective of whether we fixate one square, the other one or the surround. Yellow, red or green colours do not appear outside of the left and right contours of the squares. If binocular colour mixing were location based, we would have expected to see colours outside of the contours of the non-fixated square because this square is not located at corresponding retinal locations in the two eyes. Confinement of colour to the squares suggests that binocular colour mixing is object-based. If we keep viewing the stereogram for some time, we experience induced colours in the grey surround during monocular viewing. The induced colours are different from each other during viewing by the left and right eye. These colours are another demonstration of binocular colour induction. At the end of Section 3 we demonstrated that binocular colour induction does not depend on stereoscopic processing.

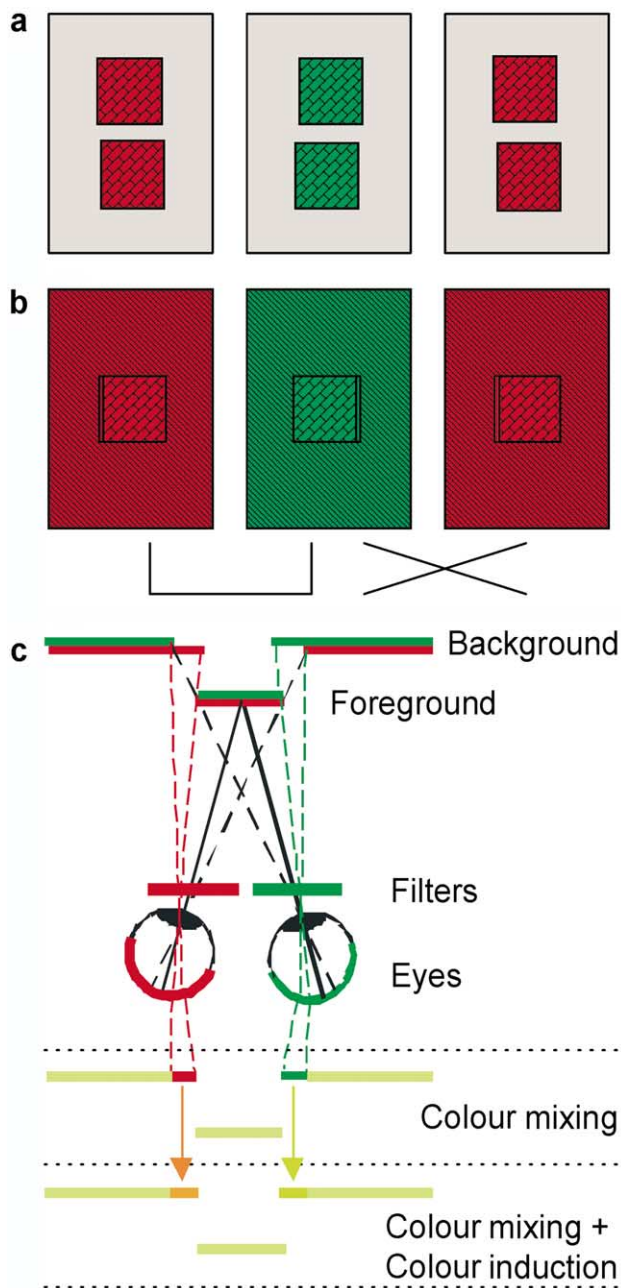


Fig. 4. (a) Stereogram with squares in two depth planes. If one square is binocularly fixated, the colour of the other square remains confined within its fused contour. The colour of the squares can be stable or alternating between red and green depending on the successfulness of binocular colour mixing. (b) Anaglyphic stereogram containing a square floating in front of a rectangular surface. (c) Top view of two eyes viewing the stereogram of (b). The stereogram is projected on a screen and dichoptically viewed by using red and green filters in front of the eyes. The scene is depicted in red in the left eye, and in green in the right eye. Two parts of the background on either side of the square, the half-occlusions, are viewed by one eye only. Binocular colour mixing predicts that the binocular part of the scene is perceived as yellow and the half-occlusions are perceived as red and green, respectively. The combination of binocular colour mixing and induction predicts that the half-occlusions are perceived as yellow too, if binocular colour induction can remove all colour differences between the two monocular representations. If not, the left half-occlusion will be slightly reddish and the right one slightly greenish.

In summary, multi-coloured stereograms unveil the existence of two binocular colour mechanisms. Binocular colour mixing is limited to binocularly fused objects whereas binocular colour induction is independent of stereopsis. Together, binocular colour mixing and induction explain why we do not perceive three clearly different colours in anaglyphic stereograms (Fig. 4b). If binocular and monocular objects differ in colour during monocular viewing, their colours will also be different during binocular viewing (see Fig. 2c). However, in the special case that binocular and monocular objects are the same colour during monocular viewing, binocular colour induction and binocular colour mixing affect the colours in similar ways so that these are hardly indistinguishable during binocular viewing.

The effects of binocular colour mixing are apparent in binocular viewing conditions only (Table 1). Furthermore, binocular colour mixing seems to be object based. These two features suggest that the mechanism responsible for binocular colour mixing receives its input from the two monocular colour representations of objects (Fig. 5). Subsequently, it reconciles differences between the colours of those objects to which the stereoscopic process designates a single representation in the binocular image. The effects of binocular colour induction are apparent during both binocular and monocular viewing. During binocular viewing it is manifest in the colours of monocular objects. During monocular viewing after binocular viewing it is manifest in the colours of all objects. These effects are explained by a mechanism that receives its input from the two monocular colour representations, measures the overall colour difference between them and subsequently reduces this difference by changing the monocular colour representations (Fig. 5).

Binocular colour induction and mixing show strikingly different dynamics. Binocular colour mixing appears and disappears immediately, whereas informal reports of the subjects indicated that binocular colour induction builds up and decays in tens of seconds or even minutes. These differences suggest the different roles of the two mechanisms in binocular vision. Binocular colour mixing assigns colours to individual objects that may become visible after a saccadic eye movement and disappear again after another. Therefore, the mixed colours should appear fast and disappear without aftereffects. In normal vision, binocular colour mixing reconciles colour differences that may occur during the viewing of near objects when certain locations of the light source can cause differences between the two monocular colour appearances. Binocular colour induction seems involved in the reduction of long-term colour differences between the left and right eye's images. Its time course suggests a slow binocular process of colour calibration that reduces colour differences between the monocular representations. These differences are

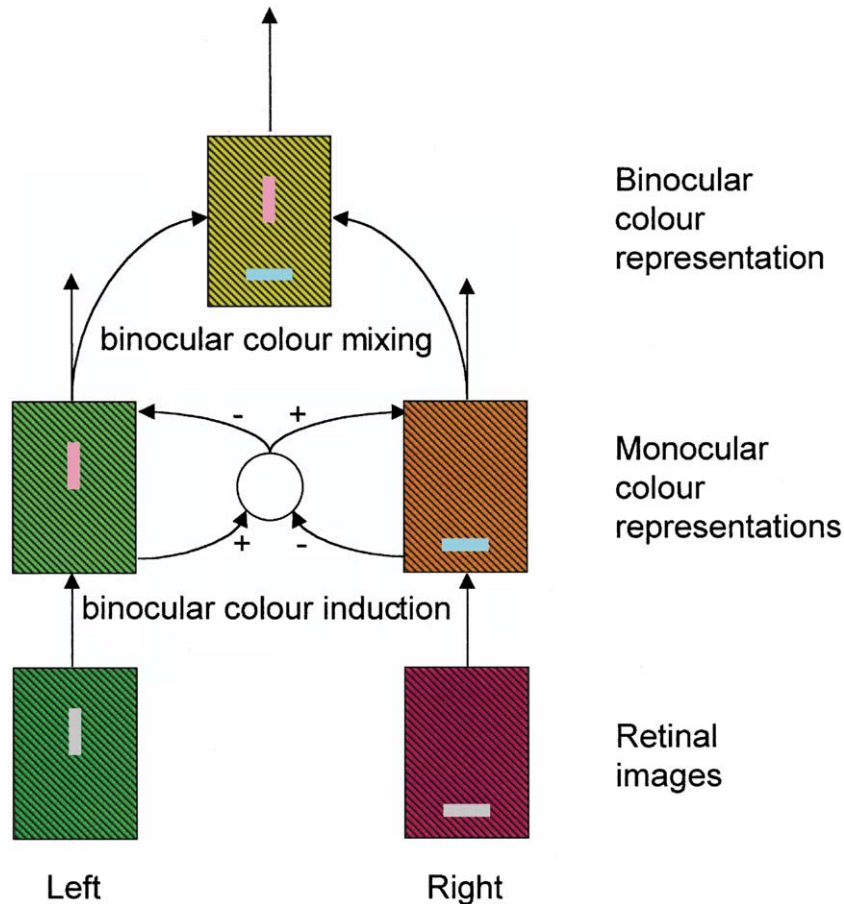


Fig. 5. Schematic model of binocular colour processing. The model contains two stages. In the first stage binocular colour induction is modelled by a feedback mechanism that reduces colour differences between the two monocular colour representations. It affects the colour appearances of both binocular and monocular objects. In the second stage binocular colour mixing converts the two monocular colours of individual objects to an intermediate binocular colour.

reduced during binocular viewing only. Calibration affects the monocular colour representations and, therefore, is also visible during monocular viewing. In normal vision, binocular colour induction may be an ongoing process of calibration that keeps the monocular colour appearances of objects adjusted to each other.

The different properties provide insight into the mechanisms that may underlie binocular colour processing. The viewing conditions and dynamics suggest that binocular colour induction is produced by a feedback mechanism, which reduces colour differences between the two monocular colour representations of the images. Several authors have reported that interocular transfer of colour adaptation requires simultaneous binocular stimulation (Delorme, 1994; Shevell & Humanski, 1984; Vidyasagar, 1976; Vimal & Shevell, 1987). These reports are consistent with the idea of colour feedback, because simultaneous binocular stimulation is an essential requirement for such a mechanism. The rationale of supposing that a feedback mechanism acts on the two monocular colour representations is that each represents the same visual world, which ideally

should be the same colour during binocular viewing and monocular viewing by either eye (Haldat, 1806; Humanski & Shevell, 1985; Vimal & Shevell, 1987). It is clear that the visual system is able to deal with conditions in which colours are different in the two eyes, viewing of stereograms being an extreme example. Binocular colour mixing is better described by a feed-forward mechanism that acts fast and does not affect the monocular colour representations.

#### 4.3. Modelling of binocular colour processing

We model binocular colour induction by a feedback loop between the two monocular colour representations of the anaglyphs (Fig. 5). Colour differences between the two representations are equally distributed over the two monocular colour representations. The transfer function of the loop is that of a first-order low-pass filter with a time constant of 3 min. Binocular colour mixing is modelled by a feed-forward loop with a response time of 0.5 s. Fig. 6 shows model simulations of binocular colour induction and mixing during binocular viewing of a

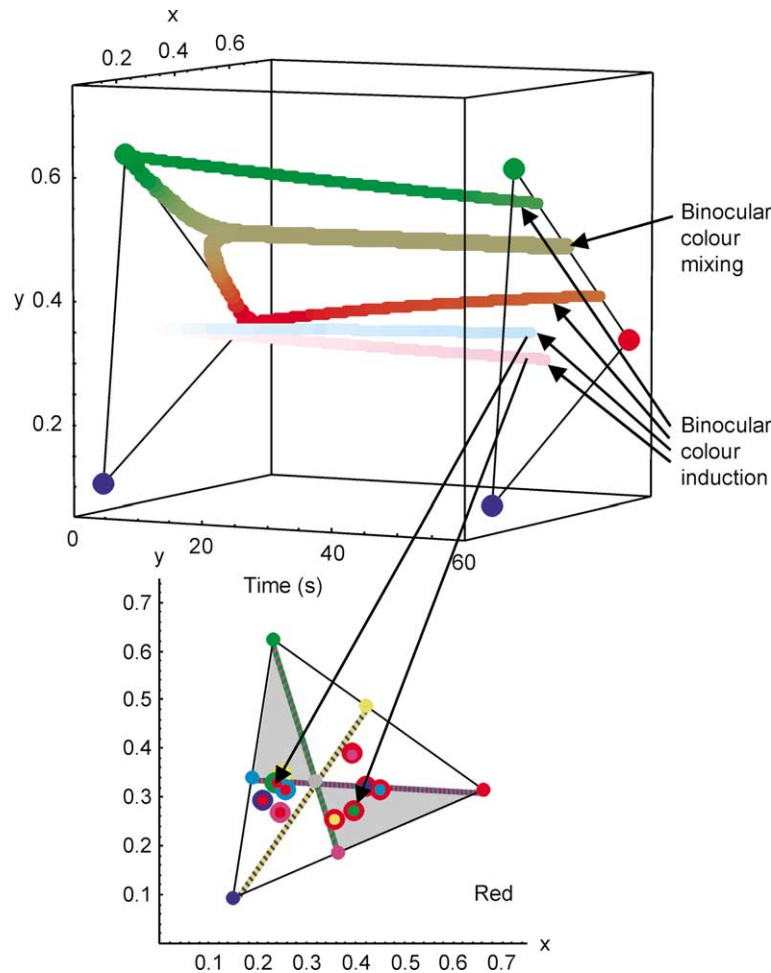


Fig. 6. Model simulation of binocular colour perception as a function of time. The stimulus is a red/green anaglyph whose images contain achromatic monocular patches. Binocular viewing starts at  $t = 0$  s. Binocular colour mixing is modelled by a fast feed-forward loop which means that the mixed colour is immediately experienced during binocular viewing. The thick curves indicate the perceived colours of the binocular part of the anaglyph as a function of time. The thin curves show how the monocular colour representations change over time due to binocular colour induction. Binocular colour induction is modelled by a slow feedback loop, which means that the induced colours build up slowly and remain visible for some time after switching from binocular to monocular viewing. The colours simulated in the monocular patches are compared with the colours measured in the matching experiment (bottom figure).

red/green anaglyph whose images contain an achromatic patch. The thick curves indicate the colour appearances of the red and green parts of the stereogram. Due to binocular colour mixing, these parts will rapidly be seen as a single, yellow coloured surface. Then the colour appearance of this surface will not change anymore. The thin red and green curves indicate the colour appearances of the red and green parts of the stereogram if binocular colour mixing is not successful. The monocular colour representations slowly change due to binocular colour induction. If binocular colour mixing operates properly, this change cannot be seen during binocular viewing. However, it becomes immediately apparent by closing one eye because then one notices that the colour appearance of the surface is different from the colour experienced before binocular viewing. Fig. 6 also shows that the achromatic patches gradually

acquire distinctive pastel colours that remain apparent during both binocular and monocular viewing.

We simulated the experimental colour matches reported in Section 3 and shown in Fig. 3. In Section 3 we reported that several subjects showed strong asymmetries between settings, depending on whether the left or the right eye viewed the patch. In the simulation shown in Fig. 6, binocular colour induction is symmetrical. This means that the feedback loop distributes colour differences into two monocular colour shifts of equal weight. Averaged over time, binocular colour induction creates straight lines in the chromaticity diagram. The orientations of the lines are related to the monocular weighting factors. If we simulate the individual differences between the settings by allowing weighting factors between 0% and 100%, we can predict that the colour matches will lie in certain areas of the chromaticity



diagram. As an example, two triangular areas, indicated by the grey colour, are shown for grey patches in red/green anaglyphs in the chromaticity diagram drawn at the bottom of Fig. 6. Areas, which are associated with different combinations of image colours, are enclosed by the following corners: the neutral point, the colour complementary to the colour of the image in which the patch is placed, and the colour of the other eye's image. The areas are either triangles or lines, depending on the combination of image colours. Examination of how many experimental colour matches (Fig. 3) are described by the model reveals that, within the tolerance of one standard deviation, all mean values (30 patches in 15 different combinations of image colours) are lying within the areas predicted by binocular colour feedback. Considering the exploratory nature of the present study, the model is only a first attempt to capture the essential properties of binocular colour induction. More sophisticated experiments will be needed to further elucidate for instance the dynamics of binocular colour induction and the conditions in which it is manifest.

#### 4.4. Binocular rivalry

When very different monocular images are presented to the two eyes, they rival for visual perception such that only one image is perceived at a time. Controversy exists whether this binocular rivalry reflects neural competition between pattern representations or monocular channels. In the light of this controversy, our present finding that binocular colour induction is manifest in rivalrous images is relevant. Neurophysiological recordings have shown that the strongest correlation between neural activity and perception is observed in the temporal lobe, whereas a strikingly large proportion of neurons in the early visual areas remain active during perceptual suppression (Logothetis, 1998; Logothetis, Leopold, & Sheinberg, 1996). These results suggested that rivalry is between the different neural representations of conflicting images rather than between the monocular channels. Recent studies, using functional magnetic resonance imaging showed strong rivalry-related responses in the primary visual cortex, suggesting that this area may be important in the selection and expression of conscious visual information (Polonsky, Blake, Braun, & Heeger, 2000; Tong & Engel, 2001).

The consequence of binocular colour induction in rivalrous images is that the two monocular channels interact. Binocular interaction is incompatible with the view that rivalry results from competition between the two monocular channels. Colour interaction suggests that the representations of monocular images still interact at lower cortical areas while they rival at higher areas. In our scheme of binocular colour processing (Fig. 5), binocular colour mixing occurs central to binocular colour induction. Cells involved in mixing are

binocular, whereas cells involved in induction are predominantly monocular. The finding that cells that were affected by rivalry were almost exclusively binocular (Logothetis, 1998) suggests that rivalry occurs at the level of binocular colour mixing rather than at the level of binocular colour induction. Reports of rivalry-related responses in the primary visual cortex (Polonsky et al., 2000; Tong & Engel, 2001) may seem to contradict this view. However, they do not because these responses may be mediated by recurrent signals. Recent analysis of response latencies of neurons in the primary visual cortex suggested that recurrent processing plays an important role in conscious visual perception (Lamme & Roelfsema, 2000; Lamme, Super, Landman, Roelfsema, & Spekreijse, 2000).

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