LOCALISATION OF COLOUR CONSTANCY; Investigation of the contribution of retinal and cortical processes in obtaining colour constancy

N.B. van der Ploeg, T.C.W. Nijboer[1] and S. te Pas[2]

Helmholtz Research Institute, Utrecht University, Utrecht, The Netherlands

[1]Supervisor

[2] Second supervisor

Abstract

There is still debate whether colour constancy is merely a result of retinal or cortical processes. In the current study, the contribution of both processes was investigated by comparing the performance of a group of colour-blind participants and controls on a colour constancy task in which object-colour associations from memory were taken along. Results show that cortical processes are most likely to be involved in obtaining colour constancy. The performance on colour constancy is comparable for both groups for natural physically coloured objects. When the colour of an object is removed, colour-blind participants, in contrast with normal observers, appear to make use of their memory (i.e. object-colour knowledge) to obtain colour constancy. Retinal input seems to be important for colour constancy to occur when there are no other visual cues available to make use of object-colour knowledge in the cortex. Furthermore, both groups showed more colour constancy for white objects with a diagnostic colour compared to non-diagnostic white objects. Apparently, those diagnostic objects are associated with a typical colour stored in memory which makes it easier to obtain colour constancy.

1. Introduction

1.1 Colour constancy

A yellow banana appears yellow whether you see it in the tungsten light of the kitchen or in the outdoors sunlight. Although the spectrum of light reflected from the banana to your retina differs under these different conditions, the banana still appears to be yellow. Colour constancy is the phenomenon in which an object's colour remains constant despite changes in the spectrum of light falling on that object, and thus changing the light reflected toward the viewer from the object (Jameson and Hurvich, 1989 in Blake and Sekuler, 2006). There are several theories about were the processes to obtain colour constancy take place; retinal (von Kries 1905; Hurlbert 1999; Pöppel 1986; van Leeuwen et al. 2006; Rüttiger et al. 2001), cortical (Zeki and Marini 1998; Walsh 1999; Kusunoki et al. 2006; Hansen et al. 2006; Gegenfurtner et al. 2008; Hurlbert and Ling 2008) or both (Land 1974; Moutoussis and Zeki, 2000).

Retinal theories

The retina consists of photoreceptors (rods and cones), which detect light and initiate neural messages to the brain. Light adaptation and colour contrast are both phenomena that have been explained to contribute to colour constancy at the retinal level. With respect to light adaptation, Von Kries (1905) suggested that adaptation mechanisms in the retina account to colour constancy. The visual system adjusts its sensitivity to the overall level of illumination. For instance, in an environment with a large amount of red light, L-cones will adapt more than the M- and S-cones. This adaptation leads to a reduction in the sensitivity of the L-cones relative to the M- and S-cones, thereby inducing colour constancy. With respect to colour contrast, Hurlbert (1999) and Pöppel (1986) promoted this as an important factor contributing to colour constancy. Hurlbert pointed to the colour contrast between objects and their background. When the illumination light changes, the wavelength light from the surface from the object and its background will also change, but their ratio of the overall spectral reflection will stay the same. As a result, the ratio of cone responses in the retina will also stay roughly the same, the encoded colour of the surface of the object will not change, and colour constancy is achieved. Pöppel (1986) also suggested that the retina contributes to achieving colour contrast. He studied a brain-injured patient whose right visual field was no longer represented in the visual cortex (incomplete homonymous hemianopia), his retinal

function was still intact. He still showed to have colour contrast. It was concluded that the lateral interactions needed for colour contrast to occur had to take place in the retina. Further support for colour constancy at the retinal level comes from a study with goldfish (Van Leeuwen, Joselevitch,, Fahrenfort and Kamermans 2006). Goldfish were trained to swim to a particular colour and still swam to that colour when the illumination light changed, indicating that they have some form of colour constancy. As they have a very small cortex and thus less cortical abilities to achieve colour constancy, retinal processes had to be involved in obtaining colour constancy. Furthermore, a study on colour constancy has been done with humans who are congenital red-green colour-blind (Rüttiger, Mayser, Sérey and Sharpe 2001). Because humans with congenital colour-blindness have difficulties in discriminating certain wavelengths, they might encounter colour constancy problems for illuminant changes along their axes of wavelength confusion. In contrast with their expectation, they found that colour-blind observers showed colour constancy very similar to that of normal trichromats along all three axes of illuminant variations (red-green, blue-yellow and natural variations in daylight). Although their variability was greater for settings along the red-green axis, they did not display a correspondingly large loss in colour constancy along that same axis. Thus, despite defected input from the retina colour-blind participants were still able to show colour constancy comparable to that of normal observers, which leads to the assumption that cortical processes might be involved in obtaining colour constancy too.

Cortical theories

The cortical processing of colour information starts with the photoreceptors which are transported via ganglion cells by the optic nerve and the optic radiation to the lateral geniculate nucleus (LGN), which further projects to the striate cortex (i.e. area V1). The area surrounding V1 is the extra-striate cortex containing many visual areas (e.g. V2, V3, V4, V5). Most studies point to area V4 as the location for colour constancy. Zeki and Marini (1998) proposed three cortical stages of colour processing in the human brain with the first stage concerned mainly with wavelength detection (V1 and V2), a second stage concerned with automatic colour constancy operations (V4) and a third stage, based on the inferior temporal and frontal cortex, more concerned with object colours. Furthermore, Walsh (1999) concluded there are several accounts of patients whose colour constancy mechanisms have failed and those with selective deficits have all suffered

damage to area V4 (Zeki, Aglioti, McKeefry and Berlucchi 1999; Kennard, Lawden, Morland, Ruddock 1995; Clarke, Walsh, Schopping, Assal, Cowey 1998 in; Walsh 1999). Other support for a role of area V4 in colour constancy comes from Kusunoki, Moutoussis and Zeki (2006) which recorded the responses of V4 colour neurons to colour stimuli and examined their chromaticity tuning in awake and anesthetized monkeys. They found that the majority of the colour-selective cells in the ventral part of V4 modulated their firing rate in a way that reflects the psychophysical colour constancy effects, i.e. they did not respond to wavelength-composition, but were colour-selective. A similar result has been previously reported in dorsal V4 of anesthetized animals (Zeki, 1983). On the other hand, Wachtler, Seijnowski, and Albright (2003) showed that V1 neurons in awake macaques were strongly influenced by chromatic spatial integration and displayed responses related to colour contrast and as a consequence, a colour constancy signal.

Other support for a cortical contribution to colour constancy comes from studies that investigate colour memory (Hansen, Gegenfurtner, Walter and Olkkonen 2006; Gegenfurtner, Hansen and Olkkonen 2008; Hurlbert and Ling 2008). Those studies indicate that the knowledge of an object's typical colour can affect an object's perceived colour. Hansen et al. (2006) used natural fruit objects to investigate colour memory. Participants had to adjust the colour of the fruit objects until they appeared gray. Their results show that the objects were perceived to be gray when they were adjusted in a direction opposite to the typical colour. At the point where the object was actually achromatic, it was still perceived as its typical colour. They concluded that natural fruit objects tend to be perceived in their typical colour, through object-colour knowledge. Gegenfurtner et al. (2008) also studied colour memory using natural fruit objects and found that the strength of the above effect depended on the degree of naturalness of the stimuli. Memory colour was largest for the most natural stimuli (with a typical colour) and decreased with decreasing stimulus realism. Although colour memory seems to play a role in achieving colour constancy, Hurlbert et al. (2008) found that colour memory is not perfect. Even without an illumination change, there was a matching error. The size and the direction of the constancy shift depended on the size and direction of the matching error based on memory alone.

Retinex-theory

Until now, theories and hypotheses have been mentioned that link colour constancy to

either retinal or cortical processes. It is, however, very well possible that both processes contribute to colour constancy. Land (1974) was the first to propose a role in colour constancy for both retinal and cortical processes, 'the retinex-theory'. He was uncertain about where the comparisons for the construction of colour would take place. Moutoussis and Zeki (2000) proposed, based on Land's retinex-theory, a two-stage mechanism involving the retina and the cortex. The first stage involves chromatic spatial integration (retinal) and the second stage occurs after the convergence of the input from the two eyes, presumably in V4, and is most likely involved in the generation of the colour percept itself.

1.2 Current study

In the current study both retinal and cortical processes that are believed to be involved in colour constancy will be investigated. The performance of retinal colour-blind participants will be compared to the performance of participants with normal colour vision. If, despite affected input from the retina, cortical processes are sufficient to obtain colour constancy participants with retinal colour-blindness will show colour constancy comparable to that of normal observers. If retinal processes are crucial for colour constancy to occur, participants with retinal colour-blindness will show abnormal colour constancy compared to normal observers. In line with the results of Rüttiger et al. (2001) the hypothesis is that participants with retinal colour-blindness will show colour constancy comparable to that of normal observers. The experiment will consist of a *Mondrian* condition, consisting of one white square surrounded by coloured squares, a *Natural Object* condition, consisting of pictures of natural stimuli-objects and a *White Object* condition, consisting of the same objects but then sprayed white. Within the latter two conditions a distinction will be made between objects with a diagnostic colour (i.e. banana, radish, pawn) and objects that can appear in various colours (i.e. candle, vase, dish brush). The hypothesis is that it will be easier to achieve colour constancy for objects with a diagnostic colour, that are believed to be associated with a typical colour stored in memory which makes it easier to obtain colour constancy (Hansen et al. 2006). The *Mondrian* condition will be compared to the *White Object* condition, to investigate the role of colour memory. The hypothesis is that participants will show more colour constancy for the *White Object* condition, because in this condition they make use of object-colour knowledge in the cortex. Additionally, the *White Object* condition will be

compared to the *Natural Object* condition, to investigate whether removing the colour of normally coloured objects influences the performance on colour constancy. In line with the results of Gegenfurtner et al. (2008), the hypothesis is that participants will show more colour constancy on the *Natural Object* condition, because those stimuli come nearest to everyday reality.

2. Methods

2.1 Participants

In total, 12 participants (mean age: 22.36, (SD = 3,35) 2 women, 10 men) with retinal colour-blindness participated in the experiment (6 red-green colour-blind; 3 deuteranope and 3 anomalous). The control group consisted of 12 participants (mean age: 23.83, (SD = 4,75), 4 women, 8 men) and had all normal colour vision as tested with the Ishihara (1971) colour plates. All participants gave informed consent and had normal or corrected to normal visual acuity.

2.2 Stimuli

A trial (see Figure 1) consists of 4 screens. First a picture of an object or square with 8 surrounding coloured squares is shown under normal white light (stimulus[1]) and secondly after a change in illumination (stimulus[2]). Presentation duration per stimulus was 3000 ms. After this, a respond screen was shown until respond followed by the fourth screen telling the participant to press the space bar before continuing the task.

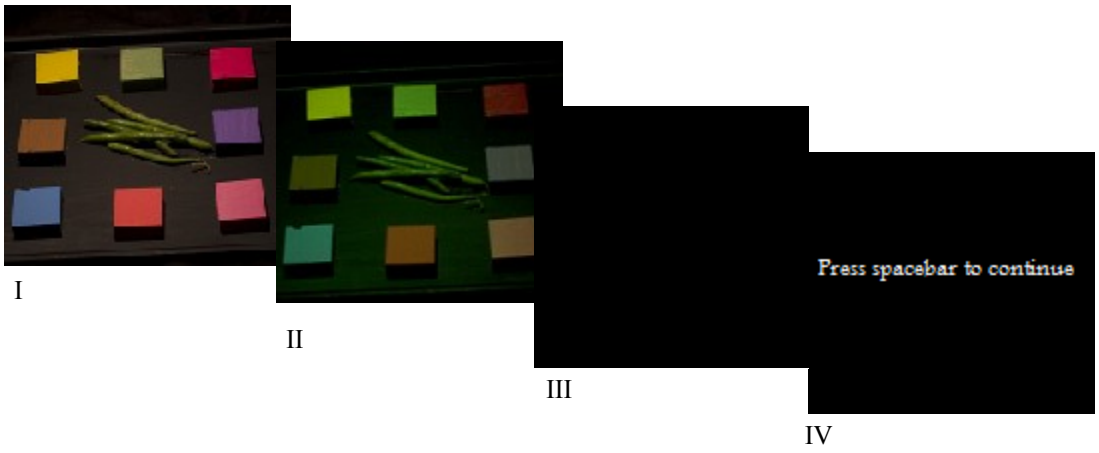

Figure 1. Design of a trial for the *Natural Object* condition, with respectively I stimulus[1], II stimulus[2] (each shown for 3000ms), III respond screen shown until respond and IV demonstrating the screen before continuing the task.

There were three experimental conditions. The *Natural Object* and *White Object* condition consisted each of 96 stimuli with objects surrounded by 8 coloured squares. The 96 stimuli of both conditions were subdivided in 48 stimuli of objects with a diagnostic colour (e.g. beans, pawn) and 48 stimuli of objects without a diagnostic colour (e.g. umbrella, pen holder). The 48 stimuli of diagnostic and 48 stimuli of non-diagnostic objects were each further subdivided in 24 congruent and 24 incongruent changes in illumination. All the objects in the *Natural Object* condition had a red, green, yellow or orange colour. For each colour there were three diagnostic and three non-diagnostic objects. The *White object* condition consisted of the same objects, but sprayed white. The *Mondrian* condition consisted of 12 stimuli of a white square surrounded by 8 coloured squares, presented in a randomized order through the *White Object* condition. The 12 stimuli were subdivided in 6 stimuli with a congruent and 6 stimuli with an incongruent change in illumination. For all three conditions, the colours of the surrounding squares were randomized.

2.3 Apparatus

The stimuli were displayed on a 22-inch laCie ZZblue III monitor with a spatial resolution of 1280 x 1024 pixels. The distance from the monitor was 57 cm and controlled for with a chin rest. A Canon Powershot SD45 camera was used to make pictures of the stimuli. Six filters (Appendix 1) were used for making the stimuli that let through different wavelengths thereby changing the illumination. Matlab with the Psychophysic Toolbox (Pelli, 1997; Brainard, 1997) was used for presenting the stimuli.

2.4 Procedure

Prior to the experiment, participants signed the Informed Consent form (Appendix 2). The experiment started with the Ishihara test for colour-blindness (1971). Additionally, participants were told that they were going to see a picture of an object surrounded by squares, followed by the same object and squares, but after a change in illumination. The change in illumination was caused by the filters that were used for making the pictures of the stimuli. Participants were asked to indicate whether the colour change of the object was congruent with its surround or not, by pressing two different keys on the keyboard. The background and the target always changed in colour (congruent or incongruent). Participants could respond after the second stimulus had

disappeared, with no limitation for the respond time. After respond a black screen was shown telling the participant to press the space-bar to go to the next trial. Participants started with five practise trials, to get acquainted with the stimuli and/or the task. Half of the participants started with the *Natural object* condition followed by the *White object* condition, which also contained the 12 stimuli of the *Mondrian* condition. The other participants accomplished the experiment the other way around. Participants were individually tested in a darkened room. The experiment lasted approximately 45 minutes.

2.5 Analysis

For all three conditions (*Natural Object* condition*, White Object* condition and *Mondrian* condition), 'Hit Rate' (HR; sum of correct responses divided by the total number of stimuli) as a measure of overall performance and the 'False Alarm Rate' (FAR; sum of congruent responses for an incongruent change in illumination divided by the total number of incongruent stimuli) as a measure of the degree of colour constancy, were calculated.

Data analysis was performed using SPSS 16.0 for Windows. First, a Repeated Measures analysis (General Linear Model) was performed for the *White Object* condition for HR and FAR separately, with diagnosticity (diagnostic versus non-diagnostic objects) as the within-subject variables and group (colour-blind participants versus controls) as between-subject variables, to investigate whether there were differences in HR and/or FAR between white-sprayed diagnostic and non-diagnostic objects.

Second, average HR and FAR were calculated for the *White Object* condition and compared to the HR and FAR of the *Mondrian* condition, with condition (white objects versus mondrians) as the within-subject variables and group (colour-blind participants versus controls) as between-subject variables, to investigate whether object-colour knowledge (from memory) influenced the performance on the HR and/or FAR.

Third, a Repeated Measures was performed for the *Natural Object* condition for HR and FAR separately, with diagnosticity (diagnostic versus non-diagnostic objects) as the within-subject variables and group (colour-blind participants versus controls) as the between-subject variables, to investigate whether there were differences in HR and/or FAR between physically coloured diagnostic and non-diagnostic objects.

Fourth, average HR and FAR were calculated for the *Natural Object* condition and compared to the HR and FAR of the *White Object condition*, with condition (*Natural*

Object versus *White Object*) as within-subject variables and group (colour-blind participants versus controls) as between-subject variables, to investigate whether object colour associations and, thereby, visual memory, influenced the performance on the HR and/or FAR

When there was a significant difference on the HR and/or FAR between the diagnostic and non-diagnostic objects in the *White Object* and/or the *Natural Object* condition the diagnostic and non-diagnostic HR and/or FAR were separately compared with either the HR and/or FAR of the *Mondrian* or the HR and/or FAR (of the diagnostic and non-diagnostic objects) of the *White Object* condition.

3. Results

3.1 Overall performance of the task based on Hit Rate

Within the *White Object* condition there was no main effect of diagnosticity ($F(1, 22) = 1.67$, $p = .210$), indicating that there was no significant difference in overall performance on the diagnostic (HR=75%) and non-diagnostic white objects (HR=77%). No interaction between diagnosticity and group was found ($F(1, 22) = 2.61$, $p = .120$), indicating that the overall performance on the diagnostic and non-diagnostic white-sprayed objects was comparable for both the colour-blind participants (HR=79% & 79%, respectively) and controls (HR=72% & 76%, respectively).

Additionally, there was no main effect of condition ($F(1, 22) = 2.06$, $p = .165$), indicating that there was no significant difference in overall performance between the *White Object* condition (HR=76%) and the *Mondrian condition* (HR=73%). No interaction between condition and group was found ($F(1, 22) = 2.67$, $p = .117$), implying that the overall performance on the *White Object* and the *Mondrian* condition was comparable for both groups (i.e. respectively, the colour-blind participants [HR=79% & 79%, respectively] and controls [HR=74% & 67%]).

Furthermore, within the *Natural Object* condition, there was no main effect of diagnosticity ($F(1, 22) = .04$, $p = .839$), showing that within the natural objects there was no significant difference between the overall performance on the diagnostic (HR=68%) and non-diagnostic objects (HR=67%).

Last, no interaction between diagnosticity and group was found ($F(1, 22) = .04$, $p = .839$), indicating that both colour-blind participants (HR=70% & 69%, respectively) and controls (HR=66% & 66%, respectively) performed comparable on the diagnostic

and non-diagnostic natural objects. A main effect was found for condition, ($F(1, 22) = 28.633$, $p \leq .001$), implying that both groups performed significantly better on the *White Object* condition (HR=76%) than on the *Natural Object* (HR=68%) condition. As seen in Figure 2, no interaction between condition and group was found ($F(1, 22) = .17$, $p = .687$), indicating that the main effect was present for both groups in the same direction, i.e. both groups performed significantly better on the *White Object* condition (HR colour-blind participants: 79%, HR controls: 74%) than on the *Natural Object* condition (HR colour-blind participants: 69%, HR controls: 66%).

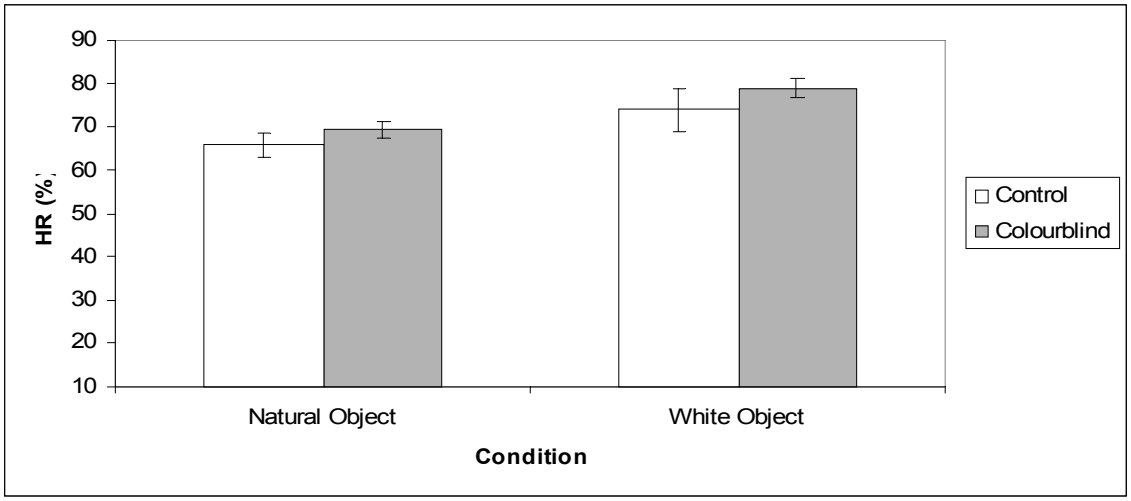

Figure 2. Hit Rates for the *Natural Object* and the *White Object* conditions for both groups.

3.2 Colour constancy performance based on False Alarm Rate

Within the *White Object* condition there was a main effect of diagnosticity ($F(1, 22) = 4{,}34$, $p = .049$), indicating that colour constancy performance was significantly better on the diagnostic (FAR=26%) than on the non-diagnostic (FAR=21%) objects (Figure 3). No interaction between diagnosticity and group was found ($F(1, 22) = .01$, $p = .919$), indicating that both groups showed better colour constancy for the diagnostic objects (FAR colour-blind participants, 26%, FAR controls 26%) than for the non-diagnostic objects (FAR colour-blind participants, 21%, FAR controls 21%). This means that the strong association between an object and its diagnostic colour is a supporting factor in obtaining colour constancy, i.e. for the white-sprayed objects.

Additionally, when comparing diagnostic white objects to mondrian, no main effect of condition was found ($F(1, 22) = .80$, $p = .383$), indicating that there was no significant difference between the performance on colour constancy on the diagnostic

white objects (FAR=26%) and the *Mondrian* condition (FAR=29%). An interaction was found between condition and group ($F(1, 22) = 6.6$, $p = .018$), indicating that the colour-blind group showed significantly more colour constancy on the diagnostic objects of the *White Object* condition (FAR=26%) than on the *Mondrian* condition (FAR=20%). For the control group this was the other way around (FAR=26% & 39%, respectively), as shown in Figure 3. This means that for the colour-blind participants the typical colour of an object contributes in achieving colour constancy compared to abstract objects.

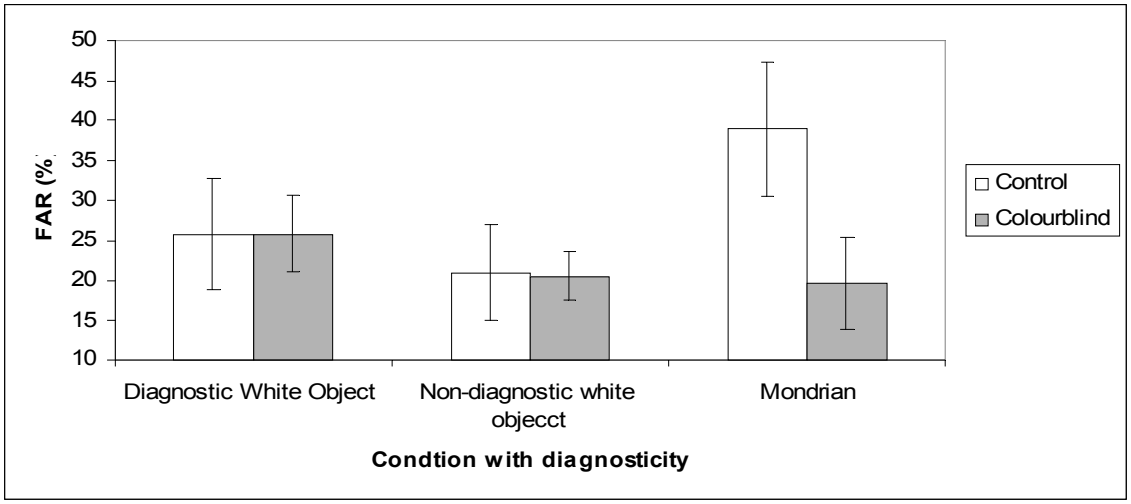

Figure 3. False Alarm Rates for the diagnostic and non-diagnostic *White Object* and the *Mondrian* condition, for both groups.

Furthermore, when comparing non-diagnostic white objects to mondrian, a main effect of condition ($F(1, 22) = 5.1$, $p = .035$) and a significant interaction between condition and group ($F(1, 22) = 6.3$, $p = .020$) was found, indicating that the control participants showed significantly more colour constancy on the *Mondrian* condition (FAR=39%) than on the non-diagnostic objects of the *White Object* condition (FAR=21%). For the colour-blind participants colour constancy for the non-diagnostic objects in the *White Object* condition (FAR=21%) and the *Mondrian* condition (FAR=20%) was comparable (Figure 3).

Last, within the *Natural Object* condition there was no main effect for diagnosticity ($F(1, 22) = 1.7$, $p = .212$), indicating that there was no significant difference on the performance on colour constancy between the diagnostic (FAR=37%) and non-diagnostic (FAR=39%) natural objects. This means that the strong association between objects and their typical colour is not a supporting factor in achieving colour constancy

for the physically coloured natural objects. No interaction was found between diagnosticity and group ($F(1, 22) = 1.6$, $p = .226$), indicating that the performance on colour constancy on the diagnostic (FAR colour-blind participants=38%, FAR controls=35%) and non-diagnostic objects (FAR colour-blind participants=38%, FAR controls=41%) in the *Natural Object* condition was comparable for both groups. As there was a main effect for diagnosticity in the *White Object* condition, they were separately compared to the diagnostic and non-diagnostic objects of the *White Object* condition. There was a main effect for the *Natural Object* condition ($F(3, 66) = 15.2$, $p \leq .001$), indicating that, overall, participants showed more colour constancy on the *Natural Object* condition (FAR colour-blind participants=38%, FAR controls=38%) than on the *White Object* condition (FAR colour-blind participants=24%, FAR controls=24%). No interaction between condition and group was found ($F(3, 66) = 0.23$, $p = .877$), indicating that the direction of the main effect was present for both groups, implying that object-colour association is a supporting factor in obtaining colour constancy for both groups.

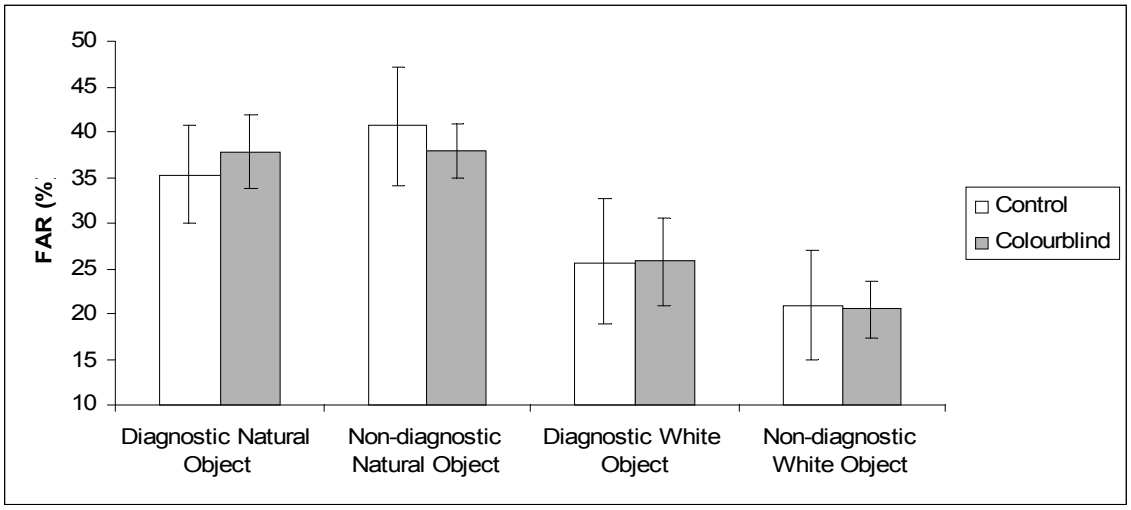

Figure 4. False Alarm Rates on the *Natural Object* and *White Object* conditions for both diagnostic and non-diagnostic objects, split by group.

4. Discussion

In the current study both retinal and cortical processes in colour constancy were dissected, to investigate were colour constancy takes place; at a retinal or a cortical level, or at both levels. To investigate whether retinal processes are involved in obtaining colour constancy participants with congenital retinal colour-blindness were included in the experiment and their performance was compared to that of participants with normal

colour vision. In line with the results of Rüttiger et al. (2001), participants with retinal colour-blindness were expected to show colour constancy comparable to that of participants with normal colour vision. Cortical processes involved in colour constancy were investigated through three conditions, i.e. the *Mondrian* condition, *White Object* condition and the *Natural Object* condition, with the latter two conditions containing both diagnostic and non-diagnostic objects.

Based on the HR as a measure for the overall performance of the task one can conclude that there were barely differences in overall performance between the two groups, indicating that both groups performed the task equally well. The only main effect found, implying that both groups performed significantly better on the *White Object* than on the *Natural Object* condition, can be explained by the fact that the change in illumination is more obvious on white objects, which makes it easier for participants to estimate whether changes in illumination are congruent with its surround or not.

With respect to the contribution of diagnostic objects on the performance on colour constancy, it was expected that the diagnostic white-sprayed objects are associated with a typical colour stored in memory, which makes it easier to obtain colour constancy for those objects compared to the non-diagnostic white-sprayed objects (see Hansen et al. 2006; Gegenfurtner et al. 2008). This implies for a cortical role in colour constancy, namely object-colour knowledge stored in memory. Both groups showed indeed significantly more colour constancy for the diagnostic white-sprayed objects. Yet, within the *Natural Object* condition, there was no significant difference on the performance on colour constancy between the diagnostic and non-diagnostic objects, for both groups. In contrast with the results of Gegenfurtner et al. (2008) showing that memory colour was largest for the most natural stimuli (as is in the *Natural Object* condition) and decreased with decreasing stimulus realism. This unexpected finding can be explained by the fact that with already physically coloured objects (as is in the *Natural Object* condition) one does not need to retrieve the colour from memory anymore and, therefore, there will be no significant difference between diagnostic and non-diagnostic physically coloured objects.

To further investigate the role of the cortex in colour memory the diagnostic and non-diagnostic objects of the *White Object* condition were separately compared to the *Mondrian* condition. Participants were expected to show more colour constancy on the *White Object* than on the *Mondrian* condition, because in the former condition

participants can make use of storage of object-colour knowledge in memory. The colour-blind group indeed showed significantly more colour constancy on the diagnostic objects of the *White Object* condition than on the *Mondrian* condition, yet for the control group this was the other way around. This unexpected finding might be explained by the study of Kraft and Brainard (in Hurlbert, 1999). They concluded that local contrast is the most important factor contributing to colour constancy. Because humans with retinal colour-blindness have difficulties in discriminating certain wavelengths, they also have more difficulties in obtaining colour contrast and therefore colour constancy. Their brain could have compensated for this by paying more attention to other visual cues than colour contrast to obtain colour constancy. Therefore, colour-blind participants might have learned to pay more attention to those other visual cues that make an appeal to cortical memory, e.g. object-colour knowledge, than normal observers do. Since the *Mondrian* condition lacks those visual cues to obtain colour constancy, colour-blind participants show significantly less colour constancy in this condition. Therefore, when there are no visual cues to make an appeal to cortical processes (as is in the *Mondrian* condition), retinal input seems to be important for colour constancy to occur. This significant difference between the diagnostic white-sprayed objects and the *Mondrian* condition, does not apply for the non-diagnostic objects of the *White Object condition.* The colour-blind group did not show significantly more colour constancy on those objects than on the *Mondrian* condition, which implies that the performance on colour constancy was comparable for those conditions. This further appears to confirm the above explanation, because those non-diagnostic objects lack the visual cues (i.e. object-colour knowledge) necessary for colour-blind participants to obtain colour constancy. The control group showed again more colour constancy on the *Mondrian* condition compared to the non-diagnostic white-sprayed objects. Yet, in line with the results of Hansen et al. (2006) one would expect that normal observers also show more colour constancy on the white-sprayed objects, than, as is the case, on the *Mondrian* condition. It could be that the size of the object plays a role. The squares used in the *Mondrian* condition were usually smaller than the objects used in the *Natural* and *White Object* condition. Hansen, Walter and Gegenfurtner (2007) studied the effect of stimulus-size on colour constancy and found indeed a high degree of colour constancy for small central test patches compared to larger test patches. This could be explained by the fact that when increasing the patch size the colour contrast between the stimulus and it's surround is restricted to the periphery,

which makes it more difficult to obtain colour contrast and thereby colour constancy. Since colour-blind participants have more difficulties in obtaining colour contrast, one would expect that this finding only yields for participants with normal colour vision, which is the case.

Furthermore, the *Natural Object* condition was compared to the *White Object* condition to investigate whether removing the colour of normally coloured objects influences the performance on colour constancy. Gegenfurtner et al. (2008) concluded that memory colour was largest for the most natural stimuli and decreased with decreasing stimulus realism, therefore it was expected that participants show more colour constancy on the *Natural Object* condition. Both groups showed indeed more colour constancy on the *Natural Object* condition, indicating that the presence of colour and the naturalness of the stimulus is a supporting factor in obtaining colour constancy.

Suggestions for further examination would be to obtain also coloured squares in the *Mondrian* condition, to investigate whether the colour in itself would be enough to obtain more colour constancy compared to the white squares in the *Mondrian* condition. Participants showed more colour constancy for the *Natural Object* condition compared to the *White Object* condition. To investigate whether this is because the stimulus contained an object or the fact that the object was coloured, abstract coloured squares need to be compared with abstract white squares. Furthermore, one could add more stimuli configurations in the *Mondrian* condition, because the number of stimuli configurations was compared to the other two conditions relatively small. When a participant made one mistake in the *Mondrian* condition, this had far more consequences on their performance on HR and/or FAR, than when the same participant made one mistake in one of the other two conditions. To control for this, their need to be a comparable amount of trials in the *Mondrian* condition as is in the *Natural Object* and *White Object* conditions.

Conclusion

Overall, in line with the results of Rüttiger et al. (2001), colour-blind participants show colour constancy comparable to that of normal observers for natural physically coloured objects. Only when the colour of an object is removed (as is in the *White Object* condition) colour-blind participants, in contrast with normal observers, appear to make use of their memory (i.e. object-colour knowledge) to obtain colour constancy. Retinal input appears to be only important for colour constancy when there are no other visual

cues available to make use of object-colour knowledge in the cortex. Cortical processes are most likely to be involved in obtaining colour constancy. With respect to the diagnosticity of an object's colour, it appears that the diagnostic white-sprayed objects are associated with a typical colour stored in memory which makes it easier to obtain colour constancy compared to non-diagnostic objects, for both colour-blind participants and normal observers.

References

Blake, R., and Sekuler, R. (2006) Color Perception, *Perception,* 5, 244-246

Brainard, D.H. (1997) The psychophysics toolbox, *Spatial Vision,* 10, 433-436

Clarke, S., Walsh, V., Schoppig, A., Assal, G., and Cowey, A. (1998) *Exp. Brain Res.* 123, 154-158

Hansen, T., Gegenfurtner, K.R., and Olkkonen, M. (2008) Colour appearance of familiar objects: effects of object shape, texture, and illumination changes, *Journal of Vision,* 13, 1-16

Hansen, T., Gegenfurtner, K.R., Walter, M., and Olkkonen, M. (2006) Memory modulates colour appearance, *Nature Neuroscience*, 9, 1367-1368

Hansen, T., Walter, S., and Gegenfurtner, K.R. (2007) Effects of spatial and temporal context on colour categories and colour constancy, *Journal of Vision,* 2, 1-15

Hurlbert, A.C. (1999). Is colour constancy real? *Current biology,* 9, 558-561

Hurlbert, A.C., and Ling, Y. (2008) Role of colour memory in successive colour constancy, *Opt. Sc. Am. A*, 25, 1215-1226

Ishihara, S. (1971) Tests for colour-blindness. Tokyo: Kanhara Shuppan

Jameson, D., and Hurvich, L.M. (1989) Essay concerning colour constancy. *Annual Reviews of Psychology, 40,* 1-22

Kennard, C., Lawden, M., Morland, A.B., and Ruddock, K.H. (1995) *Proc. R. Soc. London*

Ser. B 206, 169-175

Kusunoki, M., Moutoussis, K., and Zeki, S. (2006) Effect of background colors on the tuning of Color-selective cells in monkey area V4, *Journal of Neurophysiology,* 95, 3047-3059

Land, E.H. (1974) The retinex, *American Scientist,* 52, 247-264

Leeuwen, M.T. van, Joselevitch, C., Fahrenfort, I., and Kamermans, M. (2006) The contribution of the outer retina to color constancy: A general model for color constancy synthesized from primate and fish data, *Netherlands Institute for Neuroscience,* 24, 277-290

Martin-Elkins, C.L., George, P., and Horel, J.A., (1989) *Behav Brain Res.,* 32, 219-230

Moutoussis, K. and Zeki, S. (2000) A psychophysical dissection of the brain sites involved in color-generating comparisons, *Proceeding of the National Acadamy of Sciences of the United States of America,* 97, 8069-8074.

Pelli, D.G. (1997) The videotoolbox software for visual psychophysics: transforming numbers into movies, *Spatial movies,* 10, 437-442

Pöppel, E. (1986) Long-range colour-generating interactions across the retina, *Nature*, 320, 523-525

Rüttiger, L. Mayser, H., Sérey, L. and Sharpe, L.T. (2001) The color constancy of the red-green color blind, *Forschungsstelle für Experimentelle Opthalmologie,* 26, 209-213

Von Kries, J. (1905) Die Gesichtsempfindungen, *Handbuch der Physiologie de Menschen,* ed. Nagel, W. 109-282

Wachtler, T., Seijnowski, T.J. and Albright, T.D. (2003) Representation of colour stimuli in Awake macaque primary visual cortex, *Neuron,* 37, 681-691

Walsh, V. (1999) How does the cortex construct colour? *Department of Experimental Psychology,* 96, 13594-13596

Zeki, S. (1983) The distribution of wavelength and orientation selective cells in different areas of monkey visual cortex, *Proceedings of Royal Society London, B,* 217, 449-470

Zeki, S. and Marini, L. (1998) *Brain,* 121, 1669-1686

Zeki, S. and Moutoussis, K. (2000) A psychophysical dissection of the brain sites involved in color-generating comparisons. *Proceedings of the National Academy of Sciences of the United States of Amerika,* 97, 8069-8074

Zeki, S., Aglioti, S., McKeefry, D., and Berlucchi, G. (1999) The neurological basis of conscious perception in a blind patient, *Department of Cognitive Neurology, London,*

Appendix 1 Filters

Appendix 2 Informed Consent

KLEURWAARNEMING

Hierbij verklaar ik, ondergetekende, dat ik de instructie met betrekking tot het onderzoek '**Kleurwaarneming'** heb gekregen. Tevens heb ik de gelegenheid gehad om vragen te stellen over het onderzoek. Ik mag op ieder moment zonder een reden op te geven, stoppen met dit onderzoek.

Het is voor mij duidelijk dat het onderzoek bestaat uit één computertaak van maximaal 1 uur en dat ik hiervoor aan het eind van de test 7 euro krijg.

Ik geef hierbij vrijwillig mijn toestemming voor deelname aan het onderzoek.

Naam deelnemer: Datum:

Handtekening:

Naam experimentator: Datum:

Handtekening