

Colour-Opponent Mechanisms for the Perception of Real and Illusory Chromatic Surfaces

Colum Ó Sé

Student Identification: I6288195

One-year Master Psychology: Cognitive Neuroscience

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Location of the Internship: Faculty of Psychology and Neurosciences, Maastricht University

First supervisor: M.J. Roberts, Assistant Professor, Department of Cognitive Neuroscience,
Faculty of Psychology and Neuroscience, Maastricht University.

Second supervisor: P.H.M. de Weerd, Professor, Department of Cognitive Neuroscience,
Faculty of Psychology and Neuroscience, Maastricht University.

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Abstract

The perception of coloured surfaces depends on both the wavelength properties of the surface, and the interaction between luminance and chromaticity at the edge. This is clearly demonstrated by perceptual phenomena such as the watercolour illusion and the colour contrast effect. The primary visual cortex (V1) provides mechanisms to detect chromatic surfaces and chromatic-luminant edges, namely single and double-opponent cells. In this study, we used variations of the watercolour illusion to preferentially isolate single-opponent cells, double-opponent cells, and filling-in mechanisms. We performed a psychophysics experiment to determine how single and double-opponent cells contribute to our perception of real and illusory chromatic surfaces, and an EEG experiment to assess their electrophysiological responses to real and illusory chromatic surfaces. The results of our behavioural experiment suggest that double-opponent cells can enhance or diminish the apparent saturation of a chromatic surface through illusory filling-in and colour contrast, respectively. We observed that electrophysiological responses were largely dominated by responses to chromatic contours, while chromatic surfaces evoked weak cortical activity. The presentation of illusory and real chromatic surfaces generated equivalent cortical responses, suggesting that cortical activity at electrode Oz may be determined by perceptual rather than physical properties of colour.

Introduction

Colour perception is a complex phenomenon, determined by incident light, surface reflectance, and surrounding context (Hunt & Pointer, 2011; Hunt & Carvalho, 2016). Information from light is then processed by retinal photoreceptors and colour-opponent neurons in the lateral geniculate nucleus (LGN) and the primary visual cortex (V1; Shapley & Hawken, 2002). The role of V1 in colour perception has been highlighted since the discovery of colour-opponent neurons that detect chromatic surfaces and chromatic-luminant edges (Shapley & Hawken, 2011). Single-opponent cells are best stimulated by a uniform chromatic surface, whereas double-opponent cells respond optimally at chromatic-luminant edges and boundaries (Johnson et al., 2001; 2008; Friedman et al., 2003). While it seems plausible that chromatic surface detectors are sufficient for our perception of a coloured surface, the effects of colour contrast (Figure 1a) and illusory filling-in from surface edges (Figure 1b) cannot be accounted for by single-opponent cells alone. This has led researchers to investigate the contribution of edges to colour perception (Nunez et al., 2018; Xing et al., 2015; Zweig et al., 2015). In the present study, we use psychophysics and electroencephalography (EEG) to understand the extent to which single and double-opponent cells contribute to the perception of real and illusory chromatic surfaces.



Figure 1: *A. The colour contrast effect demonstrates the importance of boundaries for colour surface perception. Both red targets have the same wavelength spectra but the target on the equiluminant green background appears to be more saturated than the target on the red background of lower luminance (Source, Shapley & Hawken, 2011). B. The Watercolour effect (WCE; Pinna, 2001) is an illusion comprising two thin parallel contours that differ in chromaticity and/or luminance. These contours form a figure, the interior of which takes on a desaturated shade of the inner contour's hue.*

Single and double-opponent cells differ from each other in their receptive field organisation (Figure 2), and in their spatial frequency tuning. Single-opponent cells act as spatially low-

pass filters, responding optimally to chromatic surfaces that subtend visual angles less than half a cycle per degree, whereas double-opponent cells act as spatially high-pass filters and respond optimally to edges at around 2 cycles per degree of visual angle (Johnson et al., 2001 2008; Friedman et al., 2003; Livingstone & Hubel, 1984;1988). Based on their spatial tuning profiles, researchers can preferentially stimulate single-opponent cells by applying a low-pass filter to a chromatic surface, and double-opponent cells by applying a high-pass filter to a chromatic surface (Nunez et al., 2018).



Figure 2: *Single and double-opponent cell receptive fields, Source (Goldstein & Cacciamani, 2021). The single-opponent cell is cone-opponent, responding with excitation to medium wavelengths at its centre and with inhibition to long wavelengths at its surround. Double-opponent cells are both cone-opponent and spatially-opponent (Shapley & Hawken, 2011). The left side of the RF is stimulated by medium wavelengths and inhibited by long wavelengths, while this process reverses for the right side of its RF.*

In a recent study, Nunez and colleagues (2018) used a low-frequency uniform red square embedded in a grey background to isolate single-opponent cells, and a high-frequency red and grey checkerboard stimulus to optimally stimulate double-opponent cells at the chromatic-luminant edges, while minimising the contribution of single-opponent cells. As cone contrast between the target and background increased, participants perceived the checkerboard to be more saturated than the square, indicating that double-opponent cells can enhance our perception of chromatic surfaces. They also measured cortical activity using the chromatic visual evoked potential (cVEP), while participants were presented with either the checkerboard or the square stimulus during an ‘on’ period of 500ms, and no stimulus during the ‘off’ period of 1500ms. With this paradigm, the presentation of stimuli produced distinct cortical responses at the Fourier fundamental frequency (2Hz) and its harmonics. At these frequencies of interest, cVEP power was higher for the checkerboard stimulus than for the square, suggesting that double-opponent cells contributed more to the cVEP signal than single-opponent cells. Additionally, as cone contrast increased, so too did the VEP amplitude,

demonstrating that VEP amplitude rises in tandem with perceived saturation. A limitation of their stimulus set up was that the chromatic stimulus designed to attract single-opponent cells would also attract double-opponent cells at the chromatic-luminant boundary between the red square and its grey background. Consequently, a visual stimulus with smoothed edges would be more appropriate to estimate the contribution of single-opponent cells to colour perception.

The importance of edges for chromatic surface perception has received ample attention through the study of visual illusions such as the watercolour effect (Figure 1b; Pinna, 2001; Pinna & Grossberg, 2005). The contours that differ in chromaticity and luminance must be detected by neurons that respond to chromatic edges (von der Heydt & Pierson, 2006), such as double-opponent cells in V1 (Gerardin et al., 2018a). In fact, the illusion can be created by applying a high-pass filter, as double-opponent cells do, to a uniform chromatic orange surface. Therefore, double-opponent cell filtering can provide the perception of an illusory desaturated chromatic surface that would have otherwise been detected by single-opponent cells if the surface was real. While the detection of the watercolour contours may occur in V1, illusory filling-in is an extra-striate process (de Weerd et al., 1995; von der Heydt et al., 1984). Furthermore, a recent fMRI study observed that the watercolour illusory filling-in was best correlated with BOLD signals in areas V3a and V3b (Gerardin et al., 2018a).

The WCE has been studied in many psychophysics experiments that have determined that the strength of filling-in can be modulated by a variety of factors such as spatial frequency (Gerardin et al., 2014; Pinna, 2001), luminance (Coia et al., 2014; Devinck et al., 2014; Gerardin et al., 2014, 2018b), hue (Coia et al., 2014; Pinna, 2001), background (Pinna, 2001) and contour width (Devinck et al., 2014). Based on these experiments, it is now understood that the optimal watercolour stimulus is a high spatial frequency stimulus with an orange inner contour of higher luminance than the outer purple contour. This observation on contour luminance is consistent with the FAÇADE model for surface filling-in, which proposes that the purple contour forms a stronger boundary due to its higher luminance contrast with the white background, whereas the orange contour forms a weaker boundary due to its lower luminance contrast with the background (Pinna & Grossberg, 2005). When these boundaries compete, the stronger boundary formed by the purple contour inhibits the weaker orange boundary, enabling colour to spread from the orange boundary over the white surface (Pinna & Grossberg, 2005). Interestingly, braiding the watercolour contours negates the filling-in effect (Devinck et al., 2014; Gerardin et al., 2014, 2018a, 2018b), presumably because the

strength of the boundaries is equal so neither boundary becomes inhibited by spatial competition.

Coia and colleagues (2014) used an elegant EEG paradigm to isolate the contribution of the watercolour filling-in mechanism to the VEP amplitude. They exchanged visual stimuli at 4Hz to generate steady state VEPs (SSVEPs). In their experimental condition, they alternated between an illusory watercolour stimulus and a braided control, with the presentation of the illusion occurring at 2Hz. In their control condition, the braided stimuli were exchanged at 4Hz, with no change in presentation at 2Hz. Using a Fourier transform, they compared the 2Hz power between their experimental and control condition, reasoning that any difference in the 2Hz magnitude between these conditions would be due to the illusory colour. Indeed, the presentation of the illusion evoked a higher VEP amplitude relative to the control, demonstrating that the illusion generated an event-related potential (ERP; Coia et al., 2014). Additionally, the appearance of a braided stimulus with a chromatic interior also elicited a higher 2Hz VEP amplitude than the braided control, consistent with the idea that more saturated surfaces elicit higher VEP responses (Nunez et al., 2018; Xing et al., 2015). While this study demonstrated that the presentation of edge-induced illusory colour can be quantified using EEG, it remains unknown whether stimuli with defined edges detectable to double-opponent cells elicit distinct cortical responses relative to chromatic stimuli with smooth edges, designed to isolate single-opponent cells.

The aim of the present study was to use psychophysics to quantify the watercolour illusion, to assess whether filling-in also occurs on chromatic surfaces, and to determine whether the perception of edges enhances the perceived saturation of a chromatic surface. We next used EEG to determine how perception relates to cortical activity. We employed the same paradigm as Coia and colleagues (2014) to assess whether illusory and real chromatic surfaces drive a greater 2Hz amplitude relative to their respective control condition. We also compared the responses to stimuli with and without sharp edges, as a means of isolating the double-opponent cell contribution without altering the single-opponent cell response to the uniform chromatic surface. To determine whether VEP amplitude increases with the perceived saturation of stimuli (Nunez et al., 2018; Xing et al., 2015), we compared the 4Hz amplitude across our control conditions in which the same stimulus is repeatedly presented. Our hypotheses for the psychophysics and EEG experiments are depicted in figures 3 and 4, respectively.

Hypothesis 1 in the psychophysics experiment was that the watercolour illusion (WC) would be perceived at a higher saturation intensity than its braided counterpart (WCB; Figure 3). Regarding hypothesis 2, we anticipated that if both WC and WCB stimuli were filled with the same saturation intensity, participants would perceive more saturation in the filled watercolour stimulus (WCF) than the filled braided stimulus (WCFB) because illusory filling-in would also occur on chromatic surfaces. Our third hypothesis was that the appearance of edges detectable to double-opponent cells (WCSE) would enhance the apparent saturation of a chromatic surface, relative to a stimulus with smooth edges designed to preferentially isolate single-opponent cells (WCSS).

With respect to the EEG, we predicted that changes in target stimulus would evoke a higher cortical response at 2Hz in our experimental conditions (Figure 4A). In the illusory condition, we anticipated that presenting WC stimuli interleaved with WCB stimuli in the experimental condition would elicit a higher 2Hz amplitude relative to the control in which WCB stimuli were exchanged. Likewise, in the chromatic surface condition, we hypothesised that presenting the WCFB interleaved with WCB stimuli would evoke a higher 2Hz amplitude relative to the control in which WCB stimuli were exchanged, due to the presentation of a real chromatic surface. In the edges condition, we expected that presenting WCSE stimuli interleaved with WCSS would increase the 2Hz power relative to the control condition in which WCSS stimuli were alternated. Lastly, we predicted that the control condition in which WCF stimuli were alternated would elicit a higher 2Hz amplitude relative to the experimental condition in which WC and WCF stimuli were exchanged because more saturation would be perceived at 2Hz in the control condition.

Regarding 4Hz power (Figure 4B), we hypothesised that the WCF control condition would evoke the most power as it would be perceived to be the most saturated due to the perception of real colour in addition to illusory filling-in. We anticipated that the WCB control condition would elicit the least 4Hz power because no colour was perceived.

The results of our behavioural study determined that the WC target was perceived to be more saturated than its braided counterpart, and we demonstrated that illusory filling-in also occurs on chromatic surfaces. The presence of defined edges did not enhance the perceived saturation of the WCSE stimulus relative to the WCSS stimulus. In the EEG experiment, the presentation of illusory and real chromatic surfaces evoked higher 2Hz power compared to their common control condition. The presence of detectable edges did not increase the 2Hz

power relative to the control in which WCSS stimuli were exchanged. We also noted that the cortical response to real and illusory surfaces cannot be differentiated. The implications of these findings for single and double-opponent cells are reviewed in the discussion section.

Hypotheses

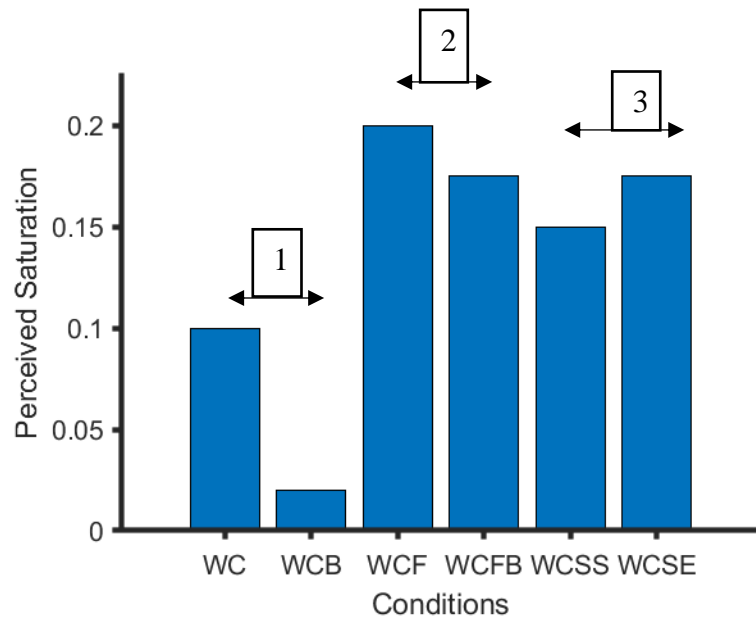


Figure 3: Psychophysics hypotheses . *1 The perceived saturation of the illusory watercolour stimulus (WC) will be greater than its braided counterpart (WCB). 2 The filled watercolour stimulus (WCF) will be perceived to be more saturated than the braided filled watercolour stimulus (WCFB), as filling-in will also occur on a chromatic surface. 3 The edges of the chromatic surface (WCSE) will enhance its perceived saturation relative to the chromatic surface with smoothed edges (WCSS).*

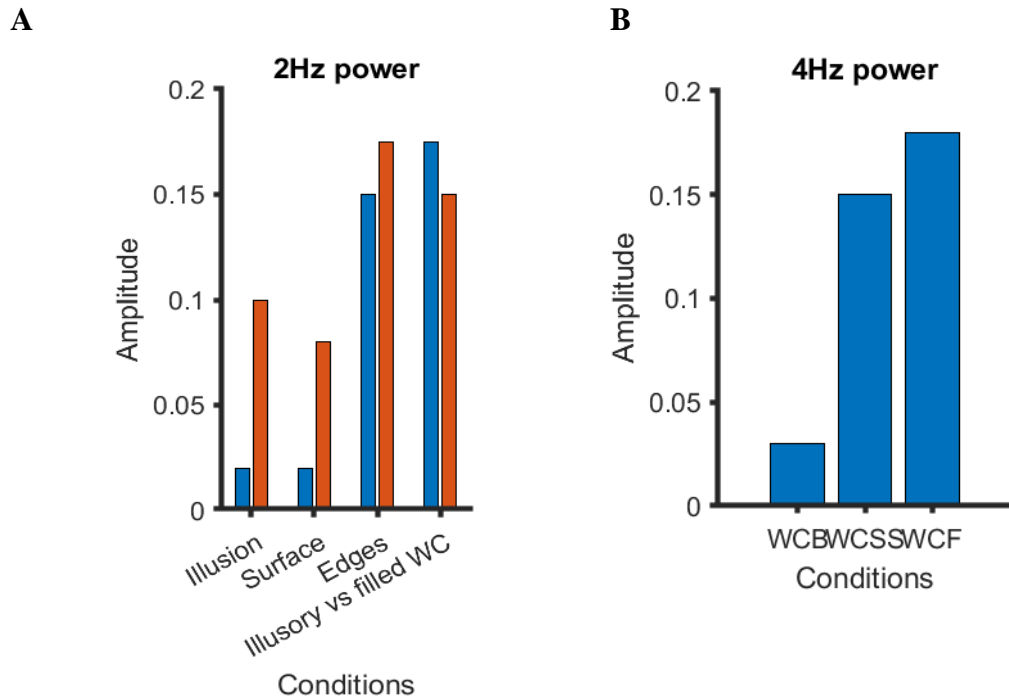


Figure 4: EEG hypotheses. **A** The anticipated 2Hz amplitudes of our experimental conditions (red), relative to their respective control conditions (blue). The names of the conditions refer to the change in target stimulus that occurs at 2Hz. We hypothesise that the appearance of the illusion, a chromatic surface, and edges in the experimental conditions will drive a higher 2Hz amplitude than their control conditions. We predict that the presentation of WCF in the control condition will evoke more 2Hz power than the WC interleaved with WCF in the experimental condition. **B** The predicted 4Hz power of our control conditions. Based on the results of Nunez and colleagues (2018), we hypothesise that the VEP amplitude will be greatest for the stimuli that are perceived to be the most saturated in the psychophysics experiment.

Methods

Participants

Twenty observers participated in the psychophysics experiment and twenty observers participated in the EEG experiment. Eight of these observers participated in both experiments. All participants provided informed consent, and the study was approved by Maastricht University's Research ethics committee, ERCPN_CODE [176_02_07_2006_V2_A1]. The participants were examined for normal colour vision using the Ishihara Plate Test.

Apparatus

In the behavioural experiment, stimuli were presented on a Samsung SyncMaster 940BF LCD monitor, which had a 1280 x 1080 display resolution and a refresh rate of 60Hz. In the EEG experiment, stimuli were presented on an Iiyama PLE2483H-DP LED monitor, which had a display resolution of 1920 x 1080, and a refresh rate of 60Hz. The luminance values and CIE xy coordinates for both monitors were obtained using a Konica Minolta Chroma Meter CS-100 A.

Visual Stimuli

Stimuli were created using Matlab toolbox R2019A (Figure 5). The visual stimuli consisted of an outer ring (diameter = 5.12°), an inner ring, and three columns within these two rings. The width and position of these columns could also vary slightly as depicted in figure 5. The rings and columns were outlined by two thin contours (2.23 arcminutes each). The area between the inner and outer ring was 13.4 arcminutes wide, the smallest column was roughly 13.4 arcminutes wide by 1.26° long, and the largest column was roughly 1.7° wide by 4° long. The white area separating the three columns was approximately 9 arcminutes wide.

We designed stimuli to isolate the colour-opponent and filling-in mechanisms for surface perception. The WC target was produced by applying a high pass filter to a black and white surface, thereby filtering the low-frequency uniform black surface. This created a grey surface bounded by black and white contours at the high-frequency edges. By replacing the outer black contour with purple, the inner white contour with orange, and the grey surface with white, we designed an illusory watercolour stimulus (WC; Figure 5). The WC target was designed to isolate double-opponent cells in addition to the filling-in mechanism. We braided the contours of the WCB stimulus to negate illusory filling-in, although the contours would be detected by double-opponent cells.

We filled the columns of stimuli 3-6 with a desaturated shade of the orange contour, creating uniform chromatic surfaces that would be detected by single-opponent cells. The WCSE and WCSS stimuli were chromatic surfaces without contours. The WCSE stimulus had defined edges that would be detectable to double-opponent cells, in addition to uniform chromatic surfaces that would isolate single-opponent cells. We applied a low-pass filter to the WCSE stimulus to create the WCSS stimulus, thus filtering the high-frequency edges that would have otherwise been detected by double-opponent cells. Therefore, the WCSS could preferentially isolate single-opponent cells.

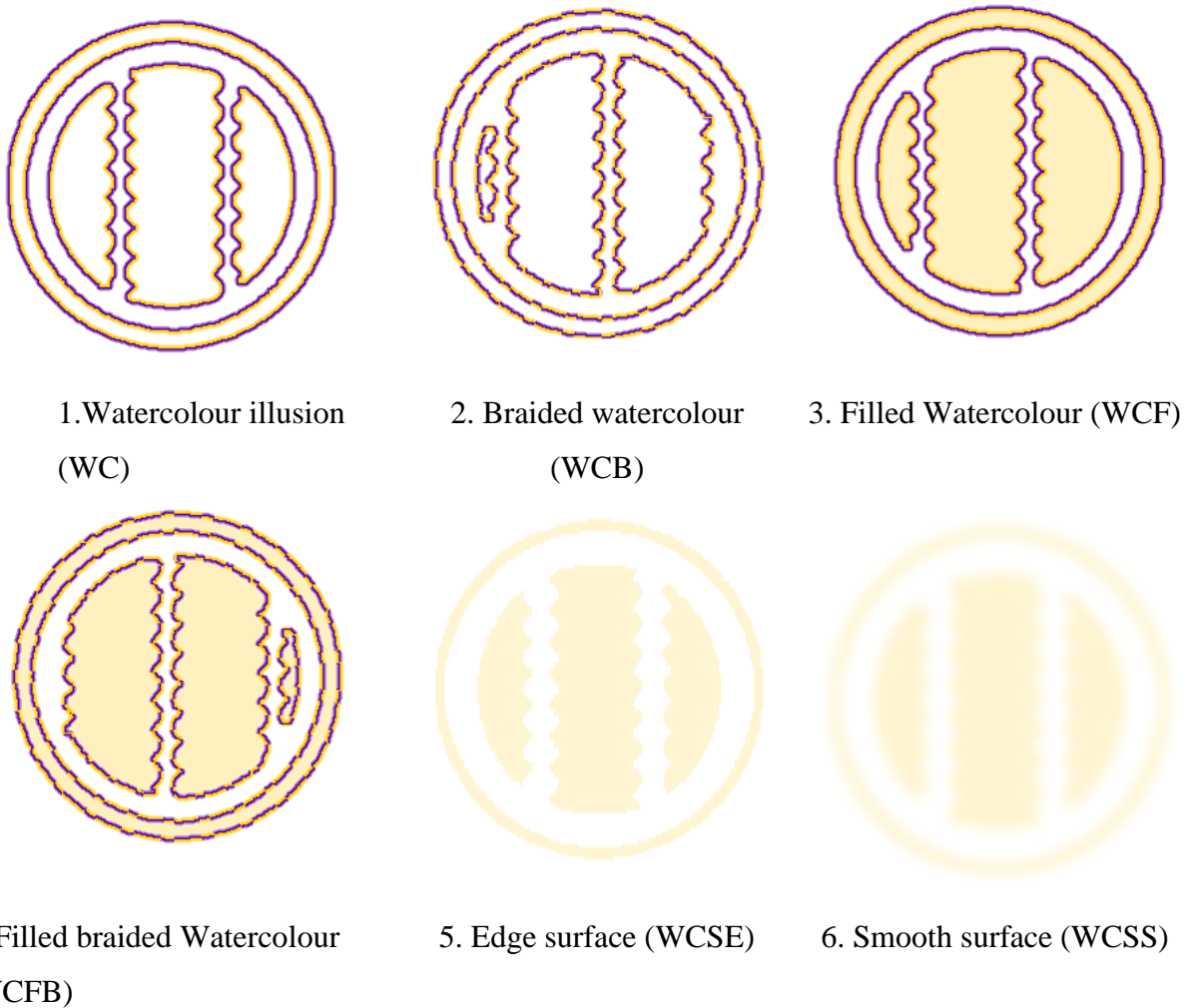


Figure 5: Visual Stimuli. Stimuli 1-4 are outlined with orange and purple contours. The columns of stimuli 3-6 are filled with a desaturated shade of orange. Note that the width and position of the columns can change.

Colour Space

We created a hue, saturation, luminance (HSL) colour space for the present study using Matlab (Figure 6). We selected RGB values for specific hues (Table 1) and drove the

phosphors from minimum to maximum luminance for the red (R), green (G), blue (B) and achromatic (A) hues. For example, the screen would appear bright red when the R gun was driven to maximum luminance. We also held the hue constant and varied the saturation intensity of the orange (O) and purple (P) hues. This demonstrated that the saturation could be modulated on a straight vector, without changing the hue. We then measured the CIE xy coordinates and luminance values at each luminance level (R, G, B, A) or saturation level (O, P) for all hues using a chroma meter. With the HSL space, the hue was held constant while we varied saturation intensity on a vector from the origin (white point) to the dominant wavelength (Figure 7).

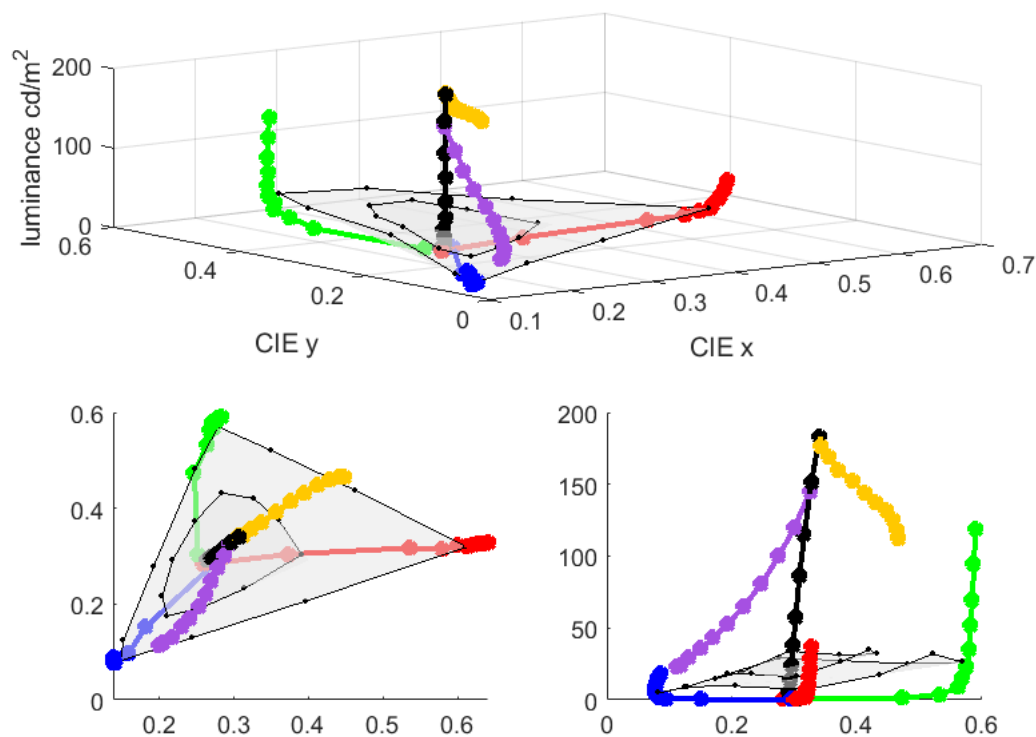


Figure 6: HSV Colour Space. The CIE xy coordinates are displayed on the x and y axes, and the luminance values are displayed on the Z axis. The luminance levels of an achromatic monitor display are depicted using the black vector. On this vector, the monitor appeared black at lower levels of luminance, and white at the highest points. All hues appeared achromatic at their first level of luminance modulation. We measured the CIE xy coordinates of the purple and orange hues as their saturation was modulated from achromatic (black vector) to fully saturated. Note that the saturation of the orange hue could be varied on a

straight vector without changing the hue. The orange and purple hues had lower levels of luminance at higher saturation intensities.

Table I: Hues and RGB values used in the colour space

Hue	R	G	B
Orange	255	207	37
Purple	166	80	226
Red	255	0	0
Green	0	255	0
Blue	0	0	255
Achromatic	0	0	0

Notes: R=Red, G=Green, B=Blue. These RGB values were used for the orange and purple watercolour contours.

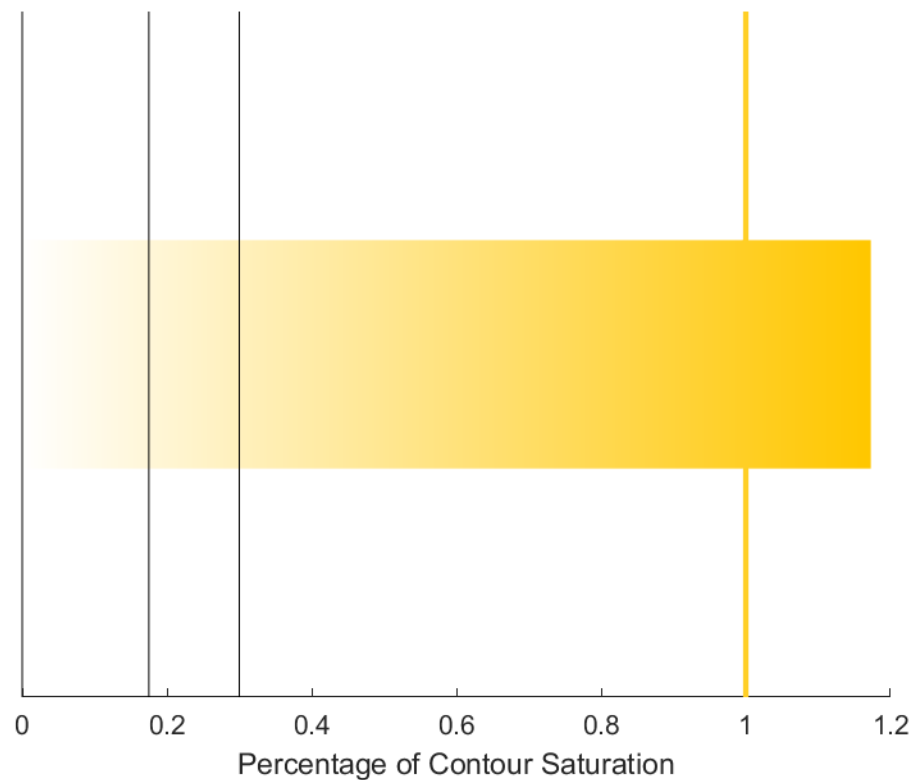


Figure 7: Saturation range for orange hue. The hue is held constant while the saturation increases from 0% (0) of the orange contour (fully desaturated), to 100% (1) of the orange contour (fully saturated). Values above 1 are multiples of the saturation of the orange contour. In the staircase task, chromatic stimuli were filled with saturation intensities of .175 along this vector as marked by the vertical line in this figure. On the first trial in a target

sequence, the two probes were filled with intensities of 0 and .3, as highlighted by the vertical black lines in the figure.

Psychophysics

The aim of the psychophysics was to quantify the perceived saturation of the watercolour illusion, and to see if braiding the contours would prevent filling-in. We also wanted to examine whether filling-in occurred on chromatic as well as achromatic surfaces, and to measure the effect of smoothing the edges on a chromatic surface stimulus, therefore limiting the contribution of double-opponent cells.

Participants were seated in a dark room, approximately 77cm from the monitor, with their head positioned upright using a chinrest. Observers completed two matching tasks, followed by a detection task. All stimuli were displayed on a white background (216 cd/m^2 , CIE $xy = 0.305, 0.339$). The outer contour of the watercolour stimuli appeared purple (15.2 cd/m^2 , CIE $xy = 0.192, 0.105$), and the inner contour appeared orange (146 cd/m^2 , CIE $xy = 0.436, 0.473$). The chromatic stimuli were filled with a saturation intensity of .175 in our colour space (Figure 7) for the matching tasks, which appeared as a desaturated orange hue (202 cd/m^2 , CIE $xy = 0.315, 0.346$).

Initially the behavioural experiments included five target stimuli, under the assumption that the filled braided watercolour stimulus was sufficient to study the edge and surface mechanisms. Once we were confident in the psychophysics tasks, we expanded our aims and included a chromatic surface with detectable edges to study these mechanisms (WCSE). Finally, twelve of the twenty observers performed the behavioural tests with all six target conditions.

Method of Adjustment

The first matching task involved a method of adjustment procedure, in which a target stimulus was presented on the monitor screen for 250ms before a probe replaced the target (Figure 8). Observers were then instructed to increase or decrease the saturation intensity within the columns of the probe stimulus using the up and down keys of the keyboard, until they were satisfied that the saturation intensity within the columns of the probe matched the saturation that they perceived within the columns of the target. This method was used to familiarise the participants with the concept of colour saturation, so that they would perceive subtle differences in saturation within the columns of the visual stimuli.

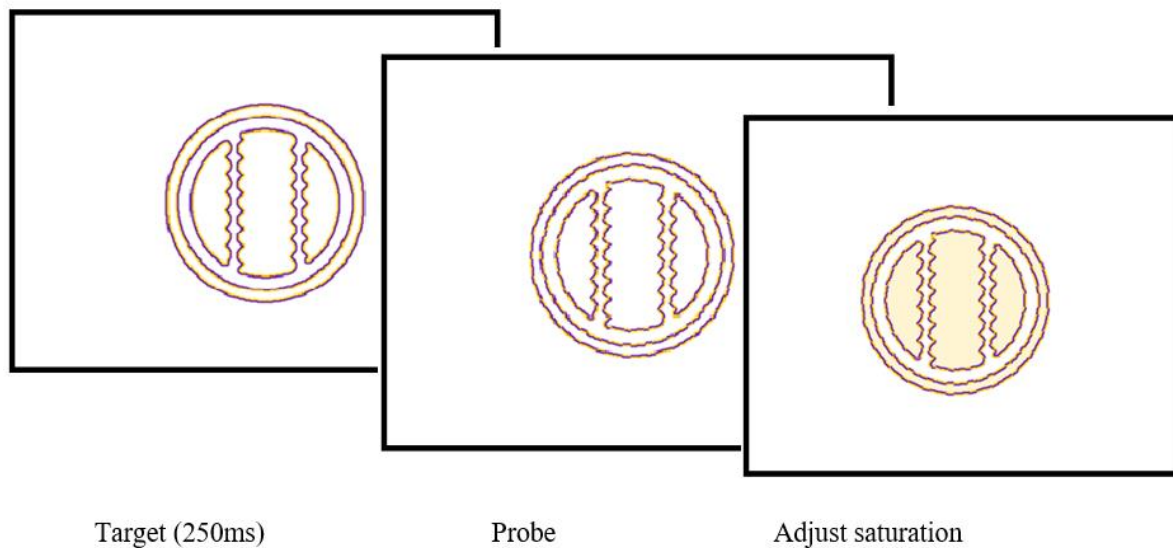


Figure 8: *Method of Adjustment. A target image is briefly presented before a probe. The participant adjusts the saturation within the columns of the probe using the up and down keys to match the saturation that they perceived within the columns of the target.*

2AFC Staircase

The second matching task was a two-alternative forced-choice staircase procedure, in which a target was briefly presented for 250ms before two probes appeared on the monitor, approximately 5° to the left and right side of the target's centre (Figure 9). There were six conditions for the staircase, each with one of the six visual stimuli as a target. For all conditions, the probes were braided watercolour stimuli which could vary in the saturation intensity of their columns based on the observer's responses.

After a target was presented, the observer was instructed to select the probe with saturation within the interior of its columns that better resembled the saturation within the columns of the target. In the first trial, the two probes were filled with different saturation intensities of the orange contour (Figure 7, Figure 9), with one being quite saturated (0.3), and the other desaturated (0). As the trials progressed for each target condition, the saturation intensity of the probes became closer in colour space, so more trials were based around the point of subjective equality (PSE) to provide a chromatic match.

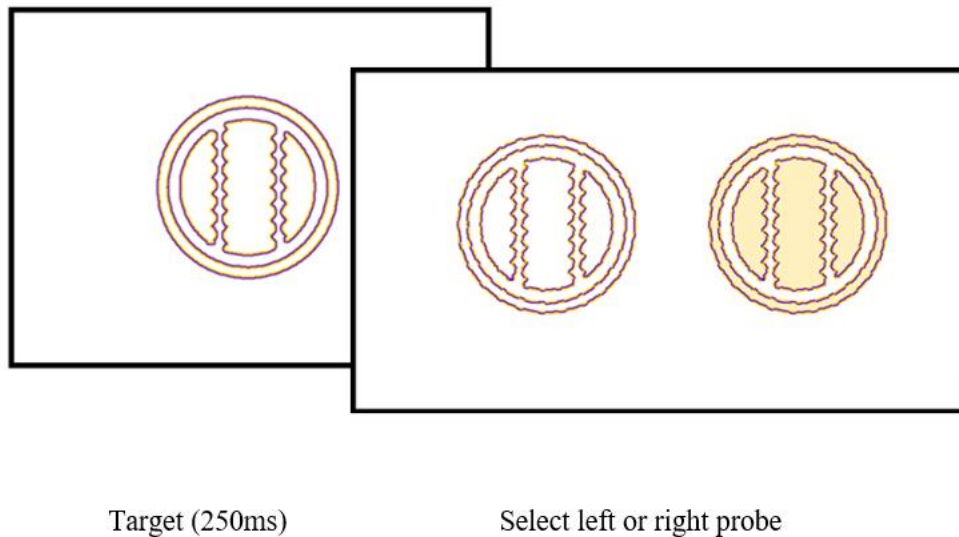


Figure 9: Staircase method. A target was briefly presented for 250ms before two probes appeared. The observer was instructed to select the probe with saturation in its columns that better resembled the saturation that they perceived within the columns of the target.

Detection task

A detection task was conducted to test if observers could differentiate between real and illusory colour (Figure 10). For this task, the chromatic stimuli were filled with the PSE saturation intensity of the illusory WC target from the staircase. Observers were presented with a sequence of stimuli for 30 seconds in a trial. Stimuli were originally presented for 250ms, although this presentation rate was too fast for participants to provide accurate responses, so the presentation rate was doubled to 500ms. The first ten of these stimuli were always the target, after which oddballs would be presented in the sequence. The oddballs had a higher or lower saturation intensity within their columns than the target. The observer was instructed to press the spacebar if they detected the chromatic oddball. The conditions of the detection task are displayed in table 2.

Table II: Detection task conditions

	Target	Oddball
Condition 1	Illusory watercolour	Filled watercolour
Condition 2	Filled watercolour	Illusory watercolour
Condition 3	Braided watercolour	Filled braided watercolour
Condition 4	Filled braided watercolour	Braided watercolour
Condition 5	Blank screen	WC Smooth surface
Condition 6	Blank screen	WC Edge surface

Notes: For conditions 1-4, visual stimuli were presented consecutively. In conditions 5 and 6, the target was a blank screen and surface stimuli appeared as oddballs.

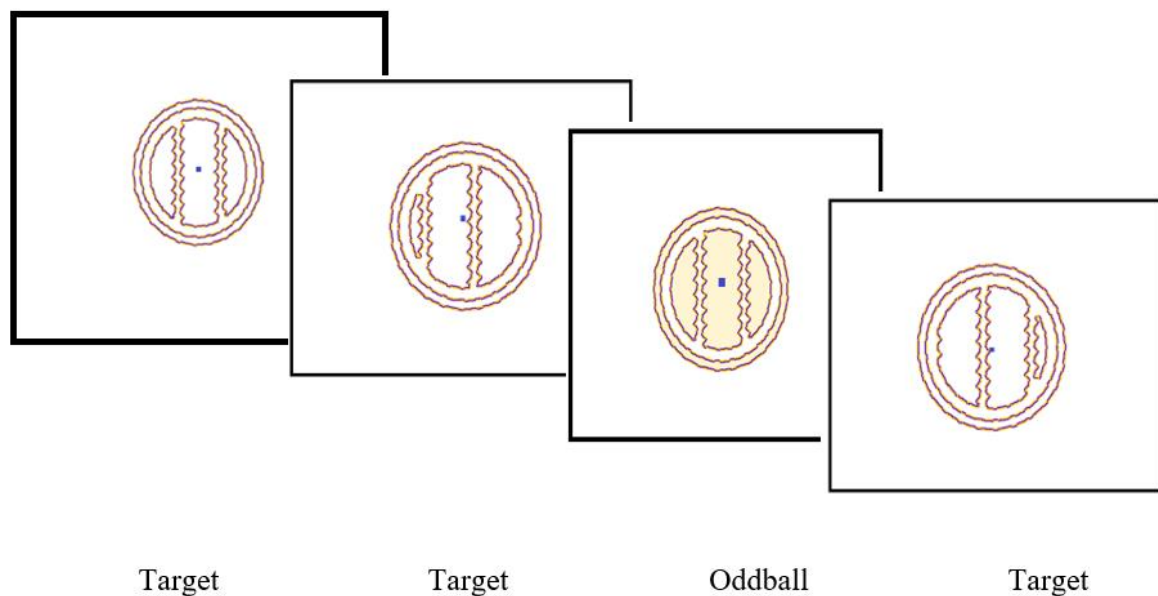


Figure 10: Detection Task. An example of condition three in the detection task. The target stimuli are WCB, and the oddball is the WCFB stimulus. The observer should press the spacebar when they detect the oddball in this sequence. Note that the column positions of targets vary slightly so the same position was never presented consecutively.

EEG

The objective of the EEG experiment was to determine whether presenting illusory and real chromatic surfaces would generate ERPs at occipital channels. We also compared the cortical responses to stimuli with and without defined edges. In our last comparison, we examined whether cortical activity would be distinguishable between an experimental condition in

which WC and WCF stimuli were interleaved, and a control condition in which only WCF stimuli were presented. We also compared the 4Hz amplitude across our control conditions to test if the 4Hz power would be proportional to perceived saturation (Nunez et al., 2018; Xing et al., 2015). We used a SSVEP paradigm to assess these ideas, as has been used in recent studies relating to the watercolour illusion (Coia et al., 2014), single/double opponent cells (Nunez et al., 2018), and the interaction between brightness and colour (Xing et al., 2015).

There were twenty participants in the EEG study, although the data from the first two participants was not included in the analysis. For these participants, we attempted to use an eye-tracker, although it failed to track the pupil in both cases. For the remaining participants, we used bipolar electro-oculograms (EOGs) to control for saccades and eye blinks. The data from these 18 participants has been included in the present study. An easy cap was placed on the participants' head with 62 Ag/AgCl electrodes laid out in accordance with the international 10-20 system (Jasper, 1958), where a ground electrode was placed at FT10, a reference electrode at TP9. The signal was originally sampled at 500Hz, and the researchers aimed to keep the impedances below 10 k Ω . The EEG signal was recorded using a BrainAmp amplifier and BrainVisionRecorder software (Brain products, Germany).

Stimulus presentation

Observers fixated on a central fixation dot while stimuli were exchanged at 4Hz, without an inter-stimulus interval. In our experimental conditions, our two stimuli of interest were exchanged so that the feature of interest was presented at 2Hz (Table 3; Figure 11). The same stimuli were alternated at 4Hz in the control conditions, with no change in target stimulus at 2Hz. It is worth noting that due to the monitor refresh rate, the presentation rate of stimuli was 4.275Hz, so peaks in power spectra amplitudes were not at exactly 2 and 4Hz.

Table III*EEG Paradigm*

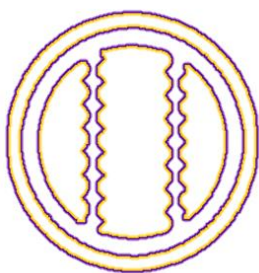
Condition		Experimental		Control	
1	Stim	WC	WCB	WCB	WCB
	Sat	0	0	0	0
2	Stim	WCFB	WCB	WCB	WCB
	Sat	$\geq .09$	0	0	0
3	Stim	WCSE	WCSS	WCSS	WCSS
	Sat	$\geq .09$	$\geq .09$	$\geq .09$	$\geq .09$
4	Stim	WC	WCF	WCF	WCF
	Sat	0	$\geq .09$	$\geq .09$	$\geq .09$

Table 3 illustrates the four experimental and control conditions that were used for the EEG experiment. Stimuli alternated every 250m, with changes in target stimulus in the experimental condition. We averaged the power of the first and second control conditions because the same stimuli were alternated. Chromatic stimuli were filled with a minimum saturation intensity of .09. Stim=stimuli, Sat=Saturation.

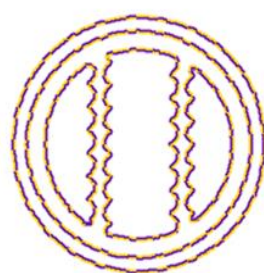
Experimental**Control**

Illusory colour at 2Hz

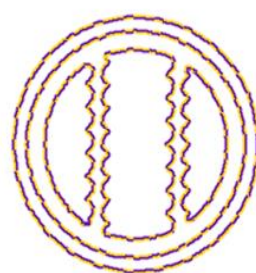
No change at 2Hz



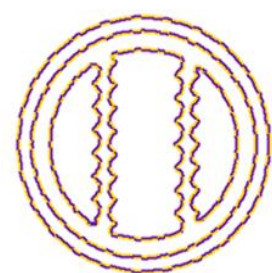
250ms



250ms



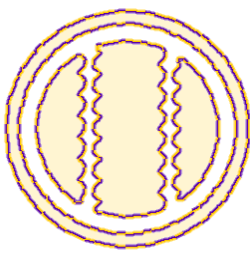
250ms



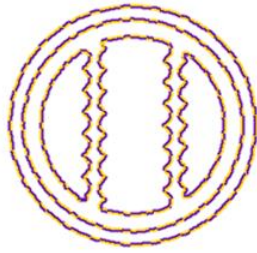
250ms

Experimental

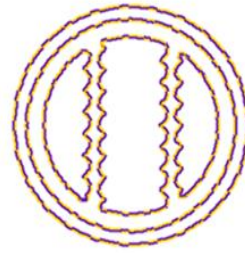
Chromatic surface at 2Hz



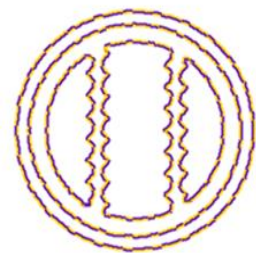
250ms



250ms



250ms



250ms

Control

No change at 2Hz

Experimental

Edge surface at 2Hz



250ms



250ms



250ms



250ms

Control

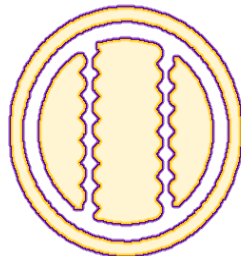
No change at 2Hz

Experimental

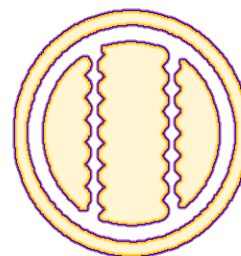
Illusory colour at 2Hz



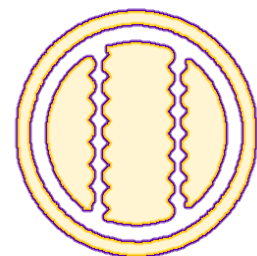
250ms



250ms



250ms



250ms

Control

No change at 2Hz

Figure 11: Experimental and Control conditions. The experimental and control conditions are depicted. Changes in target stimulus occur at 2Hz in the experimental condition.

EEG Tasks

Participants performed a short staircase task at the beginning of the experiment, using WC and WCB target stimuli. They were seated in a dark room, at a distance of 77cm from the monitor, with their head positioned upright using a chinrest. All stimuli were displayed on a white background (309 cd/m^2 , CIE $xy = .326, .372$). The outer contour of the watercolour stimuli appeared purple (14.5 cd/m^2 , CIE $xy = .226, .102$), and the inner contour appeared orange (191 cd/m^2 , CIE $xy = .457, .498$). The task consisted of four blocks, two of which had a WC stimulus as a target, and two of which had WCB stimulus as a target. The stimuli, presentation rate, number of trials, and probes were the same as that of the psychophysics staircase task.

We then personalised stimuli for each participant, by filling stimuli 3-6 with the PSE saturation intensity of the WC target from the staircase (Figure 4, Figure 9). These personalised stimuli were used in the EEG task. Participants were instructed that they should maintain fixation on the blue fixation dot, while stimuli alternated at a rate of 4Hz. Occasionally, a trial would contain a grey oddball, for which participants were instructed to press the spacebar. The purpose of this task was to maintain the observer's attention, and trials with oddballs were not included in the data analysis. If a correct hit occurred, the fixation dot would turn green for the remainder of the trial, whereas it would turn red for a false alarm (Figure 12). A trial lasted for 15 seconds, after which participants would be presented with a blink cue for one second. There were five trials in a block, after which participants were instructed that they could take a moment to rest their eyes before continuing the task. In total, there were 200 trials during the EEG task. 100 of these were for a partner project which was presented on alternate blocks.

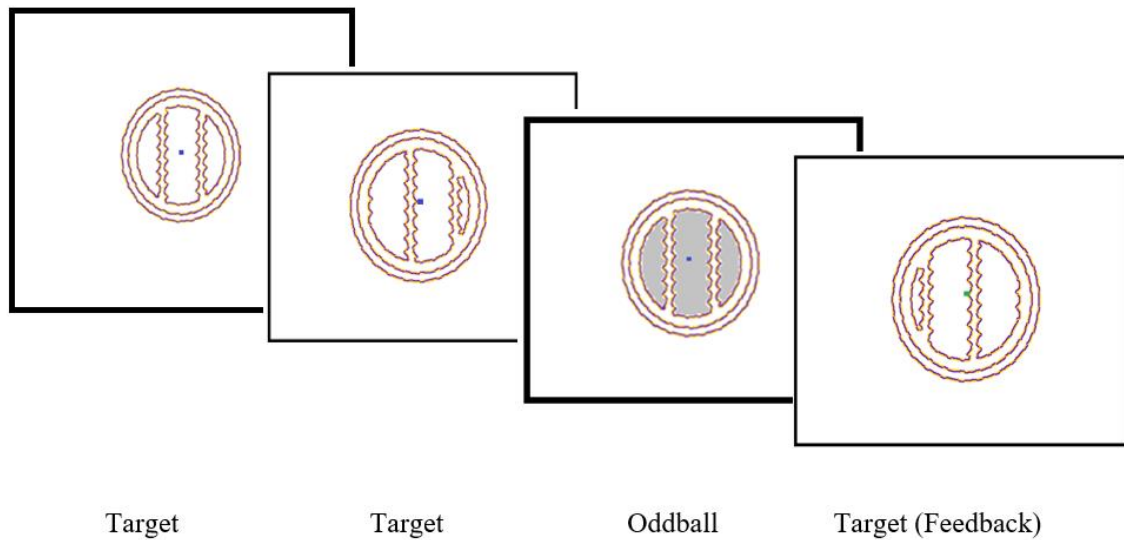


Figure 12: EEG Task. A control condition with braided stimuli is displayed. Participants were instructed to press the spacebar when they detected an achromatic oddball. The column position of targets were varied.

Data pre-processing

EEG data was pre-processed in MATLAB using the FieldTrip toolbox for EEG analyses (Oostenveld et al., 2011). All channels were re-referenced offline to an average of the left and right mastoid, TP9 and TP10, respectively. One of the hEOG channels was used to re-reference horizontal eye-movements, while its counterpart was used as an active site. This same approach was taken for the vEOG channels, leaving data from 62 channels to be pre-processed. The signal was band-pass filtered between 0.25 to 45Hz. The data was then re-sampled to 100Hz before an Independent Component Analysis (ICA) was performed. For each participant, components relating to eye-blinks were removed. We also removed noisy components, although we were cautious with component removal, as valuable data could also be lost. Therefore, components related to blinks were always removed, and other noisy components were only removed if their topography and time-course was pronounced. After removing components, we removed any remaining bad trials from the data.

Data Analysis

In the present study, we focused on activity from the Oz channel, as has been done in recent studies related to brightness and colour processing, due to its proximity to V1 (Coia et al., 2014; Nunez et al., 2018; Xing et al., 2015). Data epochs from one second after the beginning

of a trial to the end of the trial were extracted and analysed. Frequency bins were set up in steps of .05 from 1Hz to 10Hz, before a Fast Fourier Transform (FFT) was applied to the data. The data from the FFT was then grand-averaged across all participants. We focused on the 2Hz power from the FFT as changes in target presentation between our experimental and control conditions occurred at 2Hz. We also examined the difference in the magnitude of the 4Hz component of the control conditions. While no change in target stimulus (Figure 5) occurred, we anticipated that stimuli that were perceived to be more saturated would drive a higher 4Hz amplitude (Nunez et al., 2018; Xing et al., 2015).

Results

The staircase task was of primary interest to the researchers as a technique for quantifying the perceived saturation of the visual stimuli. The results of the staircase are displayed in figure 13 for all six conditions. We aimed to quantify the watercolour illusion, by comparing the perceived saturation of the WC stimulus to the WCB. Another objective was to determine whether the watercolour illusion would be effective if the white columns were filled with real colour (WCF), and whether defined edges (WCSE) would enhance the perceived saturation of a chromatic surface (WCSS). We also wanted to confirm that filling the WC and WCB stimuli produced the perception of more saturated stimuli. We made these comparisons using two-tailed paired t-tests and performed a Bonferroni correction for multiple comparisons. The perceived saturation of the WC stimulus ($M = .09$) was significantly greater than the perceived saturation of the WCB stimulus ($M = .03$, $t(19) = 5.27$, $p < .001$). Additionally, the WCF target ($M = .22$) had a significantly greater perceived saturation than the WCFB stimulus ($M = .19$, $t(19) = 3.58$, $p = .002$) at the same saturation intensity. There was no significant difference in the perceived saturation of the WCSE stimulus ($M = .25$) and the WCSS stimulus ($M = 0.24$, $t(11) = .76$, $p = .47$). Lastly, participants perceived more saturation in the WCF than the WC stimulus, $t(19) = 9.7$, $p < .001$, and more saturation in the WCFB than the WCB, $t(19) = 24.6$, $p < .001$. These results confirm that WC illusion had a quantifiable filling-in effect, that braiding the contours negated the filling-in, that illusory colour spreading also occurs on chromatic surfaces, and that sharp edges did not significantly enhance the perceived saturation of a chromatic surface. Furthermore, filling stimuli with real colour enhanced the perceived saturation of those stimuli.

We anticipated that the WCF stimulus would be perceived as the most saturated due to the presence of real colour and illusory filling-in, yet the chromatic surface stimuli (WCSE, WCSS) appeared to be the most saturated from the staircase results. To ascertain whether the high-contrast contours of the WCF and WCFB desaturated their appearance relative to the stimuli without contours (WCSE, WCSS), we performed an additional two-tailed paired t-test. We averaged the saturation of the WCSE and WCSS stimuli without contours and compared this saturation level to that of the WCFB stimulus, which had contours. We decided not to average the WCF and WCFB stimuli in this comparison as their means were significantly different, and illusory filling-in also occurs on the WCF surface. The paired samples t-test revealed that a stimulus bound by high-contrast contours (WCFB) appears

desaturated relative to chromatic surface stimuli without contours at the same saturation intensity (WCSS, WCSE, $t(11) = -3.9$, $p = .0025$).

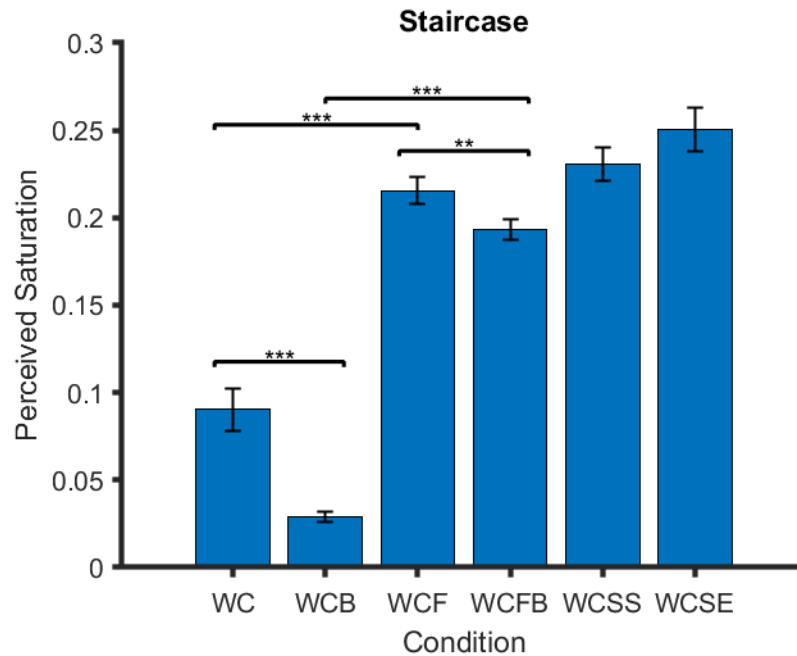


Figure 13: Staircase Results. The perceived saturation intensity for each target stimulus is plotted. 12 of the 20 observers performed the staircase task with the WCSE target. Results were accepted as statistically significant if $p < .008$, in accordance with a Bonferroni correction for six pairwise comparisons. $**p < .01$. $***p < .001$.

Detection Task

The chromatic oddballs in the detection task were filled with the PSE saturation intensity of the WC stimulus from the staircase task. Participants 16 and 20 perceived no filling-in within the columns of the illusory watercolour stimulus (.008 and .034 respectively). Due to these low saturation intensities, the PSE to the illusory stimulus appeared white. As a result, they could not perform the detection task and their results were not included in the analysis.

The results of the detection task are depicted in figure 14 for 18 participants. We anticipated that oddballs (table 2, conditions 1 and 2), with a saturation set to the PSE saturation intensity of the illusory WC target, would be harder to detect in streams of stimuli with continuous watercolour contours, as illusory colour would be perceived in addition to real colour. In

contrast, it would be easier to detect oddballs in streams of stimuli with braided contours (table 2, conditions 3 and 4), because illusory filling-in did not occur on the white surface.

We found that the peak responses occurred between 400 to 500ms after oddball onset, corresponding to around the offset of the oddball. The response rates were high across all conditions, suggesting that participants could detect oddballs with ease, regardless of whether they were chromatic or illusory. However, it is crucial to note that this may have occurred as the presentation rate in the detection task was doubled relative to the presentation rate of the staircase task, which may have inhibited the illusory colour spreading. Additionally, the staircase results demonstrated that illusory filling-in also occurs on chromatic surfaces. Therefore, the WCF stimuli that were filled with the PSE saturation intensity of the WC target from the staircase would have appeared more saturated than the WC stimuli due to the perception of real and illusory colour.

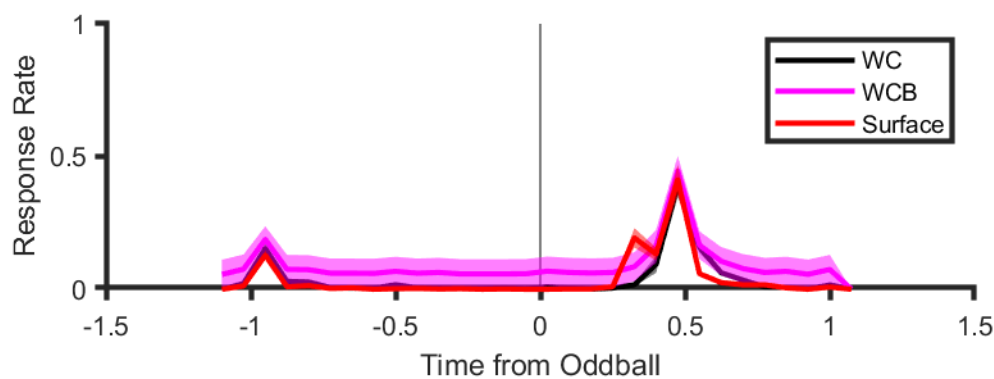


Figure 14: *Detection Task Results. Peaks in oddball detection occurred around 400-500ms after presentation. The black, pink, and red lines highlight the oddball detection rates of the watercolour (illusory and filled), braided watercolour (achromatic and chromatic), and surface (edge and smooth) conditions respectively.*

EEG

Participants performed a brief staircase task to obtain a PSE saturation intensity for the filled stimuli of the EEG task. The results of this staircase are depicted in figure 15 for 18 participants. As in the psychophysics, observers perceived significantly higher saturation in the WC ($M = .09$, $t(17) = 6.77$, $p < .001$) compared to the WCB ($M = .04$). We then filled chromatic stimuli (Figure 5, stimuli 3-6) with the PSE saturation intensity of the WC target from the EEG staircase. However, if this saturation value was below .09, we filled the

chromatic stimuli with an intensity of .09 to match the mean saturation of the WC stimulus from our behavioural experiment.

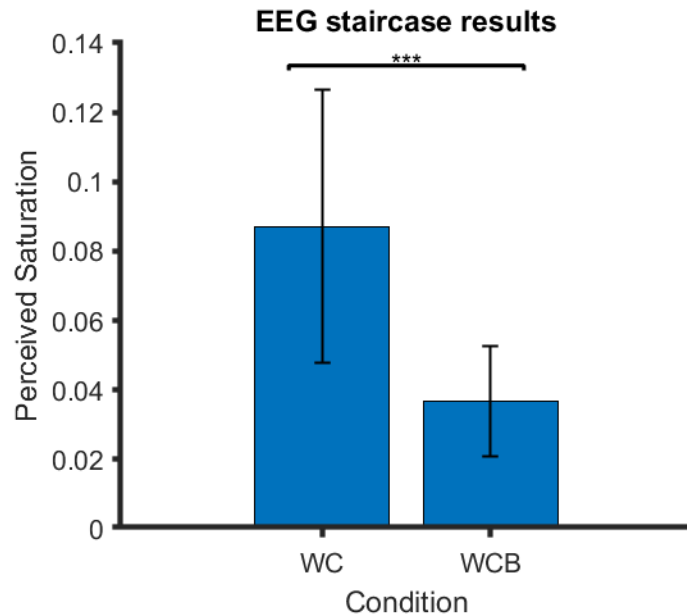


Figure 15: EEG staircase results. *** $p < .001$

Figure 16 displays the power spectra from electrode Oz for experimental (red) and control (blue) conditions. Paired t-tests were used to compare the 2Hz power of experimental and control conditions for conditions 1-4 of the EEG task. A Bonferroni correction was applied for these t-tests (four comparisons), lowering the alpha value to .0125. Topoplots show t-value maps of the comparison at 2Hz amplitude. Given the high number of channels and tests, and the relatively low number of participants, statistical tests were not applied to the topoplots. Instead, we comment only on the general trends in the t-maps.

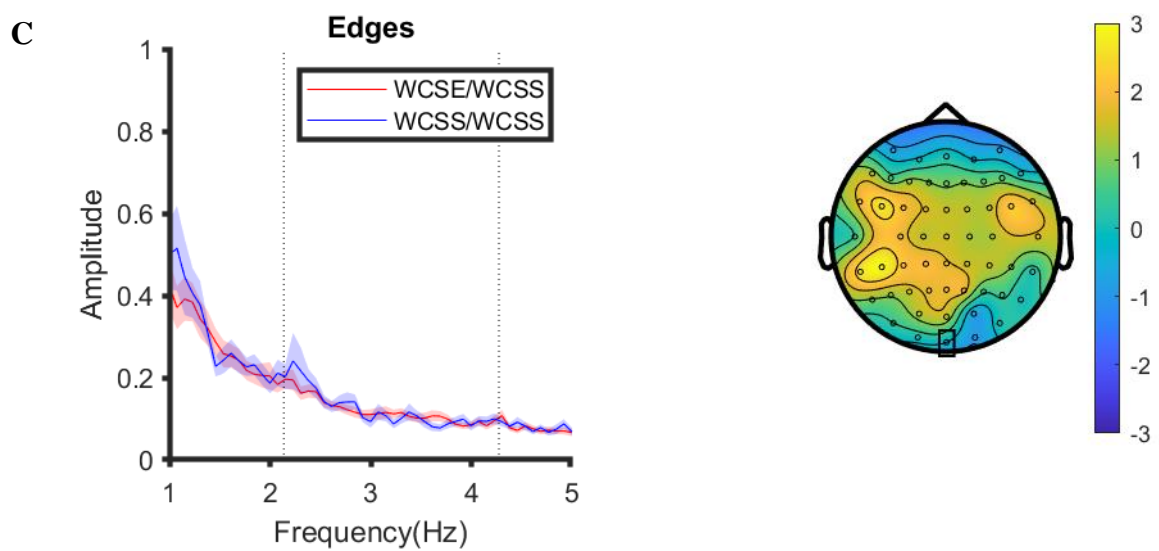
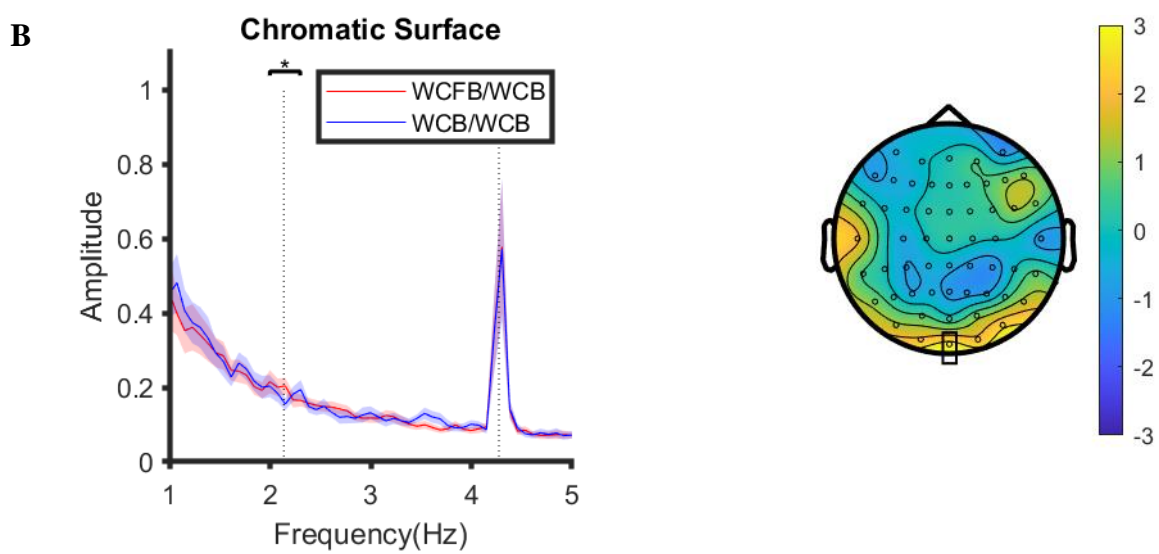
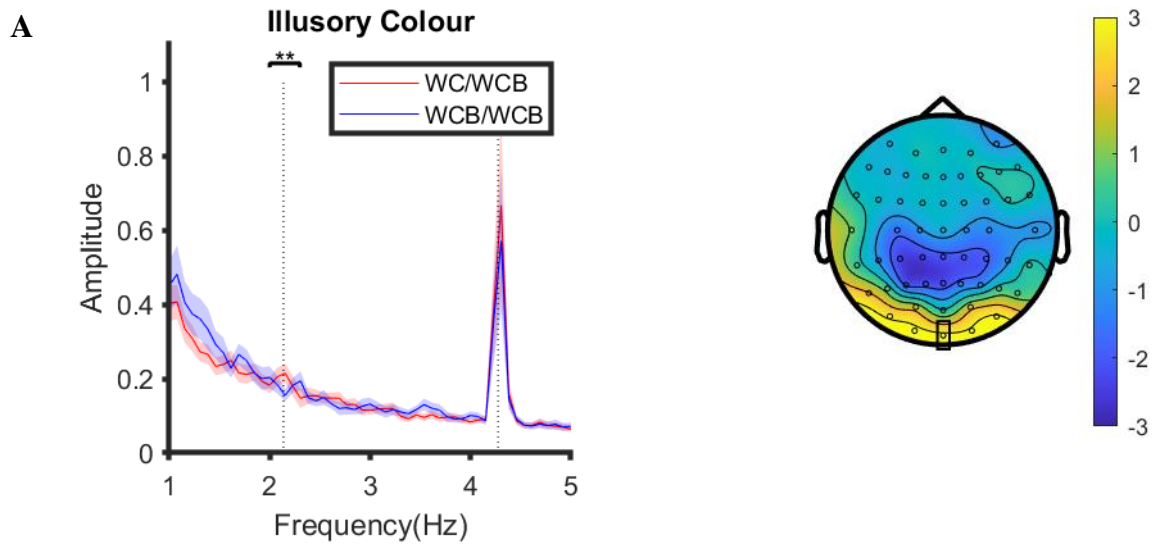
In condition 1, the presence of an illusory chromatic surface drove a significantly higher 2Hz amplitude ($M = .22$) relative to the WCB control condition ($M = .16$, $t(17) = 3.14$, $p = .0059$). Note in figure 16A that the illusion appears to elicit higher activity mainly from the occipital channels. Also note the trend of lower negative t-values in the topoplot, suggesting that the illusory surface evokes lower cortical activity in parietal areas than the WCB stimuli. Therefore, double-opponent cell-induced illusory colour leads to heightened activity in occipital areas and lower activity in parietal areas.

In condition 2, a real chromatic surface also drove a significantly higher 2Hz amplitude ($M = .2$) than the WCB control condition ($M = .16$, $t(17) = 2.8$, $p = .0125$). The chromatic surface elicited similar activity at occipital channels relative to the illusory chromatic surface, although the increased activity does not appear to be as widespread across occipital channels (Figure 16B). Interestingly, there is not a trend towards lower negative t-values in the parietal areas as was the case when the illusion was presented at 2Hz. Thus, single-opponent cell-induced real colour evokes a similar cortical response as double-opponent cell-induced illusory colour, albeit not as widespread across occipital channels.

In condition 3, the presence of edges did not significantly increase the 2Hz power, $t(17) = -.26$, $p = .8$. Note that for this condition, the presence of sharp edges elicited a very similar activation pattern at occipital channels (Figure 16C). In fact, differences in the activation patterns of experimental and control conditions appear across parietal and mid-frontal areas, where the presence of sharp edges appears to evoke more cortical activity. Ultimately, the double-opponent cell activation in response to the sharp edges does not differ at occipital channels relative to the single-opponent cell activation to smooth surfaces.

In the 4th condition, the appearance of an illusory WC target did not drive a significantly different 2Hz amplitude relative to the WCF target in the control condition, $t(17) = .37$, $p = .7$. There also appears to be little difference in activity at the occipital channels, although slightly more activation across parietal and frontal channels, suggesting that WC and WCF surfaces evoke similar cortical responses, despite the presence of real colour in the WCF stimulus (16D). Therefore, the addition of single-opponent cell-induced colour to the WCF target did not significantly enhance the cortical response to the double-opponent cell-induced illusory colour in the experimental condition.

To summarise, the presence of edges did not increase the 2Hz amplitude, although the presentation of real (WCFB) and illusory (WC) chromatic surfaces did enhance the power at the Oz channel. Interestingly, the appearance of the illusion and of sharp edges caused activation patterns in parietal areas. Additionally, there was no distinguishable cortical response between illusory (WC) and filled (WCF) stimuli in the fourth condition.



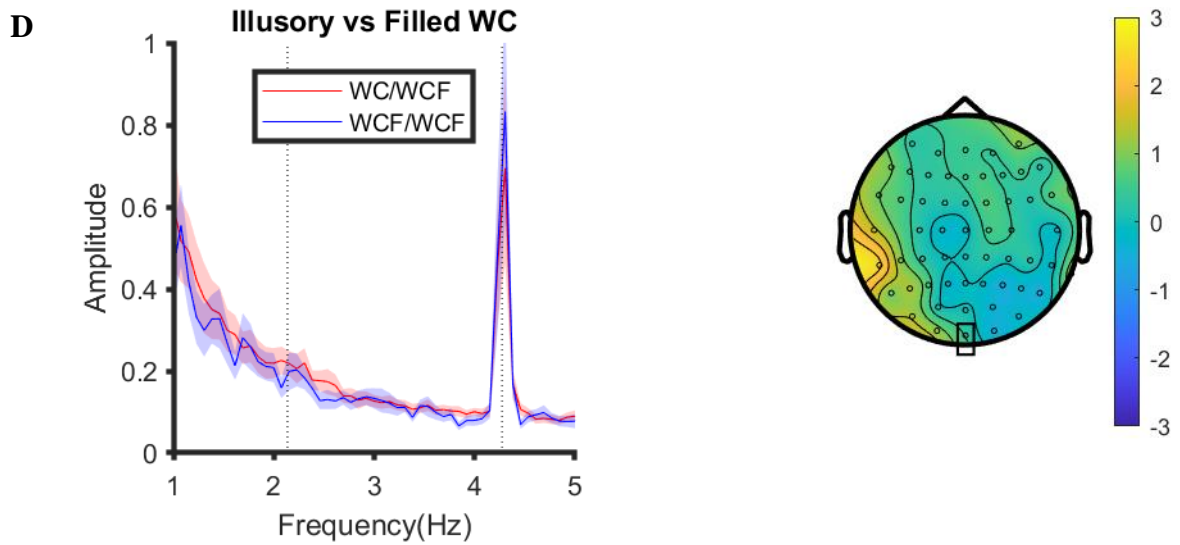


Figure 16:Power spectra and t -value maps of conditions 1-4. Figure titles reflect the changes in target stimulus that occur at 2Hz in the experimental (red) and control (blue) conditions. The power spectra data is from electrode Oz, as highlighted in the topoplots. The difference in 2Hz power across all channels is displayed to the right of each power spectrum. Higher positive t -values are mapped in yellow and lower negative t -values are mapped in blue. A= Condition 1, B= Condition 2, C= Condition 3. * $p < .01$ ** $p < .01$.

Figure 17 depicts a bar chart with the averaged 2Hz power across the experimental and control conditions. Note that illusory and real chromatic surfaces (Figure 16A & 16B) elicit very similar 2Hz power in the experimental conditions, and that the presence of edges has little impact on the 2Hz power relative to its control condition in which WCSS stimuli were exchanged.

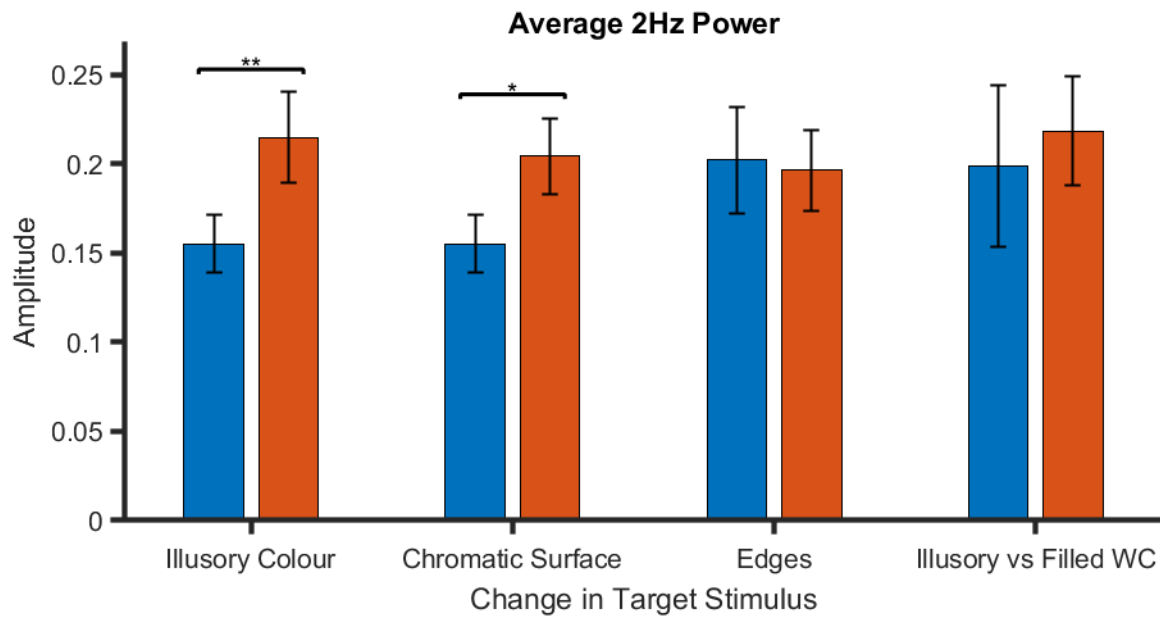


Figure 17: Average 2Hz Power across Conditions. Condition titles reflect changes in target stimulus that occurred at 2Hz in the experimental conditions. A bar chart with the averaged VEP at 2Hz is displayed. Experimental conditions (red) are plotted beside their respective control conditions (blue). * $p < .05$ ** $p < .01$.

In conditions 1 and 2 (Figure 16A & 16B), the appearance of illusory and real colour at 2Hz increased the power relative to their common control condition in which WCB were alternated. It is worth noting once again that WCFB was filled with the PSE saturation intensity of the WC target for each participant. Therefore, both surfaces should have appeared equally saturated. A comparison was made between these experimental conditions, to determine whether they elicited different cortical responses (Figure 18). The presentation of illusory and real colour elicited similar 2Hz power in their experimental conditions, $t(17) = .8$, $p = .43$ (Figure 18A). Note in figure 18B that the illusory surface appears to elicit slightly higher cortical activity at occipital channels, and lower activity at parietal channels relative to the real chromatic surface. Ultimately, double-opponent cell-induced illusory colour and single-opponent cell-induced real colour evoke similar cortical responses.

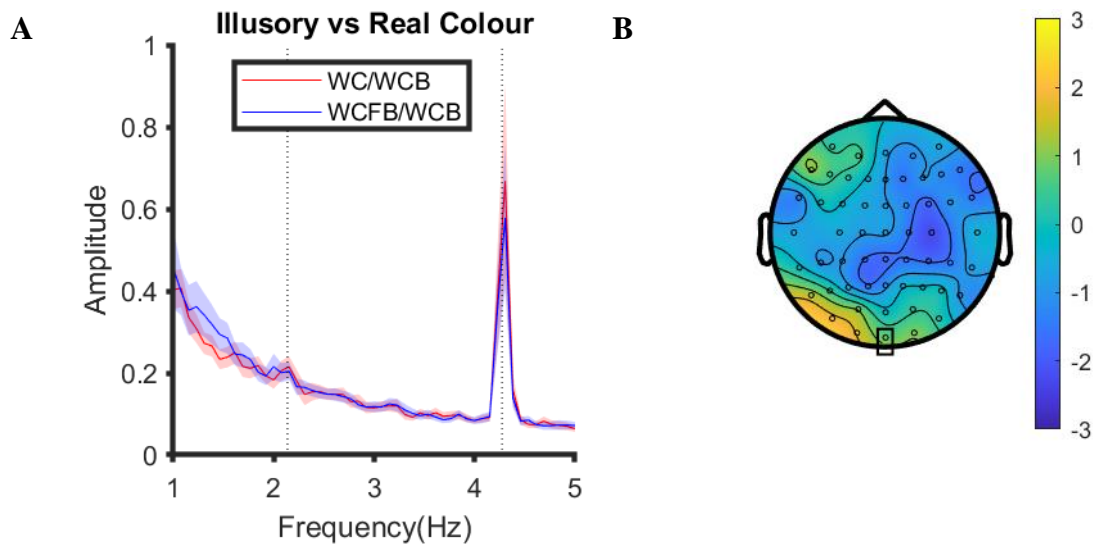


Figure 18: Power spectrum and *t*-value map of a comparison between experimental conditions 1 and 2. An illusory surface is presented at 2Hz in condition 1, whereas a real chromatic surface is presented at 2Hz in condition 2. The power spectrum data is from channel Oz, as highlighted in the topoplot. There is little difference in the *t*-values of the experimental conditions across channels, demonstrating that illusory and real colour evoke similar cortical responses.

Figure 19 illustrates the power spectra and average 4Hz power of the control conditions, in which the same stimulus was repeatedly presented. Note the peak in the power spectra of the WCF and WCB control conditions at 4Hz, whereas the WCSS condition drove a steady VEP amplitude. A repeated measures ANOVA was performed to ascertain whether there were differences in the means across the three control conditions. Mauchly's test of Sphericity determined that sphericity had been violated, $X^2(2) = .094$, $p < .001$. A Greenhouse-Geisser correction was applied to correct for this violation of sphericity, by adjusting the degrees of freedom. The results of the correction determined that there was a statistically significant difference in the 4Hz power between at least two of the three conditions, $F(1.5, 17.8) = 7.434$, $p = .013$. Subsequently, post-hoc analyses with Bonferroni corrections were performed to ascertain which of the conditions differed in their power at 4Hz. The post-hoc analyses revealed that the WCF control condition ($M = 0.55$) evoked a significantly greater 4Hz amplitude than the WCSS control condition ($M = 0.09$, $p = .036$), and the WCB control condition ($M = 0.41$, $p = .022$). There was no statistically significant difference in the 4Hz power between the WCB and WCSS control conditions ($p = .68$). From the average 4Hz power across control conditions (Figure 19B), it appears as if the WCSS evoked a weak VEP

amplitude. The smoothed edges of the WCSS stimulus preferentially isolated single-opponent cells, whereas the contours of the WCF stimulus would have been detected by double-opponent cells. This would suggest that a great deal of the WCF stimulus power, which was also filled with the PSE saturation intensity of the WC stimulus, was evoked from the double-opponent cell detection of contours and illusory filling-in. Topoplots (Figure 20) depict t-value maps of the control condition comparisons at 4Hz amplitude. In 20A and 20B, it appears as if the contours of the WCF and WCB stimuli elicit higher cortical activity across all channels relative to the WCSS stimulus.

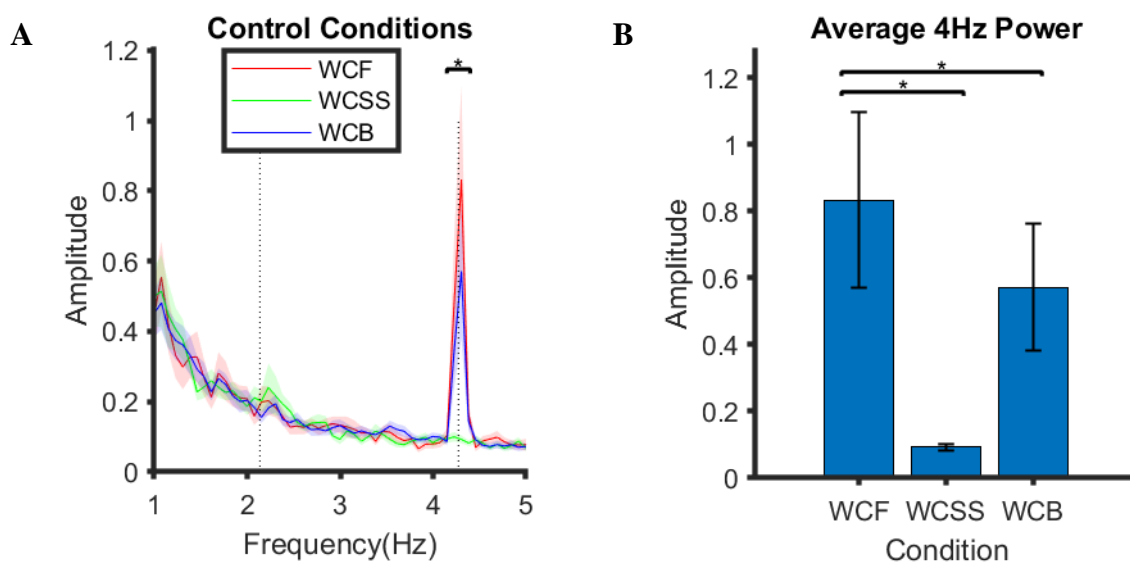
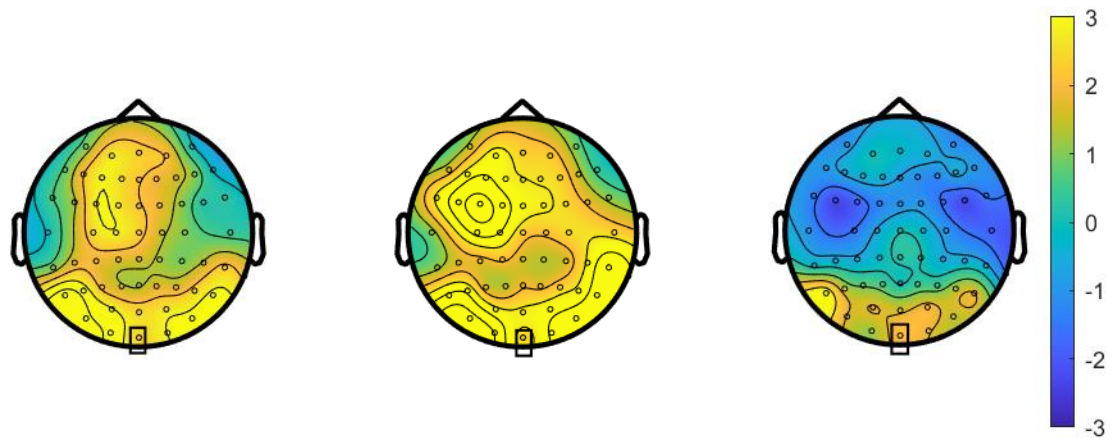


Figure 19: Power Spectra and Average 4Hz Power of Control Conditions. **A.** The power spectra of control conditions. Peaks in amplitude occur at 4Hz for the WCF and WCB stimuli, while the amplitude of the smooth surface stimulus remains flat. **B.** The average 4Hz power of control conditions are presented in a bar chart. * $p < .05$.



A **B** **C**

Figure 20: Topography of differences in 4Hz power between control conditions. A=WCF-WCSS, B=WCB-WCSS, C=WCF-WCB. Yellow corresponds with higher positive t -values, whereas blue corresponds with lower negative t -values.

Discussion

We performed a psychophysics experiment to determine how single and double-opponent cells contribute to our perception of real and illusory chromatic surfaces, and an EEG experiment to assess their electrophysiological responses to real and illusory chromatic surfaces. We hypothesised that the illusory WC would be perceived to be more saturated than its braided counterpart, that illusory filling-in occurs on chromatic as well as achromatic surfaces, and that the double-opponent cell detection of edges magnifies the apparent saturation of a uniform chromatic surface. Additionally, we hypothesised that changes in target stimulus would be reflected by an increase in the 2Hz VEP amplitude, and that the 4Hz power of control conditions would be proportional to the perceived saturation of visual stimuli.

In our psychophysics experiment, the watercolour illusion had a quantifiable filling-in effect. As in previous studies, we found that braiding the contours of the illusory stimulus prevented filling-in (Devinck et al., 2014; Gerardin et al., 2014, 2018a, 2018b). Interestingly, we established that the watercolour spreading also occurs on chromatic surfaces, as observers perceived more saturation within the WCF stimulus relative to the WCFB stimulus. Therefore, double-opponent cells can enhance the perceived saturation of visual stimuli by integrating information about the chromaticity and luminance of continuous contours at the borders of a surface.

To our surprise, the presence of defined edges on a chromatic surface (WCSE), did not increase its apparent saturation relative to its counterpart with smoothed edges (WCSS). This result fails to support our expectations based on previous literature (Nunez et al., 2018). Therefore, we cannot draw the same conclusion as Nunez and colleagues, that double-opponent cells enhance the perceived saturation of chromatic surfaces. However, unlike Nunez and colleagues (2018), we smoothed the edges of the stimulus that was designed to preferentially stimulate single-opponent cells (WCSS), so that no edges would be detected by double-opponent cells. This may account for the discrepancy between the results of the two studies. It is also worth noting that the luminance contrast between target and background was the same for both WCSE and WCSS. Therefore, perhaps double-opponent cells require contrast at the edges to influence our perception of chromatic surfaces.

Another surprising result was that the chromatic surface stimuli (WCSS, WCSE) were perceived to be more saturated than the WCFB stimulus, despite being filled with the same

saturation intensity. This finding may be explained by the effects of colour contrast (Figure 1a). When encompassed by a boundary of unequal luminance, a chromatic target takes on a more desaturated appearance (Faul et al., 2008; Shapley & Hawken, 2011; Xing et al., 2015). The purple and orange contours of our chromatic stimuli (WCF, WCFB) were of lower and higher luminance, respectively, than the luminance of the chromatic surface. This luminance contrast may have desaturated the appearance of these target stimuli. Therefore, the WCFB stimuli that we used as probes would have appeared to be more desaturated than their true saturation intensity of .175. Consequently, these probes would require a higher saturation intensity within their columns to match targets without high-contrast edges (WCSS, WCSE).

The objective of the detection task was to ascertain whether participants could differentiate between real and illusory colour. We found that detection rates across all oddball conditions were high, although this is likely due to our finding that illusory filling-in also occurs on chromatic surfaces. Therefore, the WCF stimulus would have the PSE saturation intensity of the illusory WC target from the staircase task, in addition to the illusory filling-in.

Consequently, it is likely that the WCF oddballs would stand out as being considerably more saturated in streams of WC target stimuli.

In the EEG experiment, we anticipated that changes in target stimulus would increase the 2Hz power of experimental conditions. Similar to Coia and colleagues (2014), we found that the presentation of illusory (WC) and real chromatic surfaces (WCFB) increased the 2Hz magnitude of their experimental conditions relative to their respective control conditions in which WCB stimuli were exchanged. It is worth noting that these target stimuli (WC, WCFB) were also perceived at a higher saturation intensity than the WCB stimulus in the staircase task. This would indicate that the higher 2Hz VEP amplitude may have captured changes in perceived saturation, in addition to changes in target stimulus.

The presentation of defined edges (WCSE) did not alter the 2Hz power relative to its control condition in which WCSS stimuli were exchanged. While changes in target stimulus occurred at 2Hz in the experimental condition, it is possible that no change in perceived saturation transpired. Indeed, in the psychophysics, the presence of detectable edges did not increase the perceived saturation of the chromatic stimulus compared to the WCSS. Consequently, it is possible that the similarity in 2Hz power between the experimental and control condition reflects the comparable perceived saturation of the stimuli. Furthermore, these results would suggest that edges detectable to double-opponent cells do not enhance the perceived

saturation of chromatic surfaces nor do they increase cortical activity in response to chromatic surfaces. Therefore, it is likely that double-opponent cells require more information about chromaticity and luminance contrast at boundaries to influence cortical activity.

There was also no significant difference in the 2Hz power of the experimental condition in which WC and WCF stimuli were interleaved, and its control in which WCF stimuli were alternated. However, the results of the staircase demonstrated that observers perceived a difference in saturation between the two stimuli. Additionally, participants could distinguish between WC and WCF oddballs within their respective streams in the detection task. This finding would suggest that while observers can differentiate between real and illusory watercolour stimuli, the cortical activity between the two cannot be differentiated.

Lastly, there was no difference in the 2Hz power between our first two experimental conditions in which illusory colour (WC) and real colour (WCFB) were interleaved with WCB stimuli. Interestingly, the WCFB stimulus was filled with the PSE saturation intensity of the WC target from the staircase for each participant. Therefore, the changes in target stimuli in both experimental conditions should have evoked the perception of equally saturated columns at 2Hz. Once again, this demonstrates a link between the perceived saturation of stimuli and the electrophysiological response to stimuli. It also highlights that double-opponent cell-induced illusory colour and single-opponent cell-induced real colour elicit similar cortical responses. Thus, it may not be the colour-opponent mechanisms that influence cortical activity at electrode Oz, but rather our perception of colour.

Based on previous literature (Nunez et al., 2018; Xing et al., 2015), we hypothesised that the VEP amplitude would be proportional to the perceived saturation of stimuli. Following this logic, we reasoned that the WCB control condition would elicit a weak 4Hz response, due to the appearance of an achromatic surface. We anticipated that the WCSS control condition would drive a higher 4Hz amplitude due to the presentation of a chromatic surface. Contrary to our hypotheses, the WCSS elicited the lowest mean 4Hz response of all control stimuli. This effect may have occurred as the cVEP is spatially-tuned, with low-frequency stimuli eliciting weak responses (Rabin et al., 1994; Tobimatsu et al., 1995). In other words, low-frequency chromatic stimuli, such as uniform chromatic surfaces designed to stimulate single-opponent cells (WCSS), are known to drive weak VEP responses.

Interestingly, albeit unsurprising given the spatial tuning of the cVEP, the WCF 4Hz amplitude was significantly greater than the amplitude of the WCSS stimulus. In the former, the chromatic-luminant edges of the contours would be detected by double-opponent cells, which induce an illusory filling-in, while its real chromatic interior would be detected by single-opponent cells. The chromatic surface of the WCSS would be detectable only to the single-opponent cells, due to the smoothed edges. Therefore, the power difference between the two stimuli would have occurred through the double-opponent cell detection of contours, and double-opponent cell-induced filling-in. This would be in line with the findings of previous research, that neuronal responses to achromatic and chromatic surfaces in macaque V1 are largely dominated by responses at the edges, presumably by double-opponent cells (Zweig et al., 2015).

In conclusion, the objective of our study was to investigate the relative contributions of single and double-opponent cells to colour surface perception. We hypothesised that the WCSS, which was designed to preferentially isolate single-opponent cells, would evoke less perceived saturation and lower cortical activity relative to its counterpart with edges detectable to double-opponent cells (WCSE). In fact, both stimuli evoked the perception of equally saturated chromatic surfaces and equally high electrophysiological responses. Considering this observation, low-pass mechanisms like single-opponent cells provide us with sufficient information about the saturation of a chromatic surface. In that case, if high-pass mechanisms like double-opponent cells do not aid the perceived saturation of a chromatic surface, what do they contribute to colour vision?

We propose that double-opponent cell responses to boundaries do not inherently enhance the perceived saturation of chromatic surfaces, nor do they increase cortical activity. Rather, double-opponent cells enable the interaction between luminance and chromaticity at the edges of chromatic surfaces, which can influence the perceived saturation and cortical responses to surfaces. As was observed in the present study, when double-opponent cells integrate information from continuous contours differing in chromaticity and luminance, illusory filling-in occurs over a surface. Therefore, double-opponent cells do not influence colour perception by detecting edges, but rather by integrating chromaticity and luminance signals at the edges between a surface and its background.

The interaction between chromaticity and luminance can also hinder our perception of a chromatic surface through colour contrast effects (Figure 1a). This effect occurred in the

present study, as participants perceived a stimulus with high-contrast contours (WCFB) to be less saturated than stimuli without contours (WCSE, WCSS), despite the chromatic surfaces being filled with the same true saturation intensity. However, when there is no luminance contrast between target and background, the apparent saturation of the target is enhanced (Faul et al., 2008; Shapley & Hawken, 2011; Xing et al., 2005). To our knowledge, it remains unknown why a luminance contrast between a chromatic surface and its background appear to desaturate the appearance of the surface. Previous studies have used equiluminant chromatic gratings to isolate double-opponent cells (Johnson et al., 2001, 2008), so it is unknown how such neurons respond when the luminance of a chromatic grating is modulated. Consequently, it is uncertain whether the colour contrast effect emerges through a decrease in double-opponent cell activity, or by inhibition of the single-opponent cell surface response. Researchers could explore the former possibility non-invasively, by recording VEP activity while modulating the luminance of high-frequency chromatic gratings. Considering the observation in our study that double-opponent cell-induced filling-in leads to enhanced perceived saturation and cortical activity, likewise we would anticipate that because double-opponent cell-induced colour contrast diminishes perceived saturation, cortical activity would also decrease with an increase in contrast. Indeed, this was also observed in a recent study by Xing and colleagues (2015), in which their red target appeared most saturated, and evoked the highest cortical activity when it was displayed on an equiluminant grey background.

To summarise, we investigated the contribution of single and double-opponent cells to real and illusory colour surface perception. Single-opponent cells act as low-pass filters to provide us with the perception of a uniform chromatic surface. Contrary to previous researchers, we argue that double-opponent cells do not enhance the apparent saturation of chromatic surfaces through edge-detection. Rather, we propose that double-opponent cells facilitate the interaction between chromaticity and luminance at boundaries, which can enhance the perceived saturation of a surface through illusory filling-in or diminish its apparent saturation through colour contrast. Our findings demonstrate that real and illusory chromatic surfaces generate equivalent cortical responses, suggesting that cortical activity at electrode Oz may be determined by perceptual rather than physical properties of colour. Finally, we observed that the cortical responses to stimuli in our study were largely influenced by responses to the edges, where chromatic contours were present. This implies a greater contribution of double-opponent cells than single-opponent cells to electrophysiological activity.

References

- Coia, A. J., Jones, C., Duncan, C. S., & Crognale, M. A. (2014). Physiological correlates of watercolor effect. *Journal of the Optical Society of America. a, Optics, Image Science, and Vision*, 31(4), 15–22. <https://doi.org/10.1364/JOSAA.31.000A15>
- De Weerd, P., Gattass, R., Desimone, R., & Ungerleider, L. G. (1995). Responses of cells in monkey visual cortex during perceptual filling-in of an artificial scotoma. *Nature*, 377(6551), 731–4.
- Devinck, F., Gerardin, P., Dojat, M., & Knoblauch, K. (2014). Spatial selectivity of the watercolor effect. *Journal of the Optical Society of America. a, Optics, Image Science, and Vision*, 31(4), 1–6. <https://doi.org/10.1364/JOSAA.31.0000A1>
- Gerardin, P., Devinck, F., Dojat, M., & Knoblauch, K. (2014). Contributions of contour frequency, amplitude, and luminance to the watercolor effect estimated by conjoint measurement. *Journal of Vision*, 14(4). <https://doi.org/10.1167/14.4.9>
- Gerardin, P., Abbatecola, C., Devinck, F., Kennedy, H., Dojat, M., & Knoblauch, K. (2018a). Neural circuits for long-range color filling-in. *Neuroimage*, 181, 30–43. <https://doi.org/10.1016/j.neuroimage.2018.06.083>
- Gerardin, P., Dojat, M., Knoblauch, K., & Devinck Frédéric. (2018b). Effects of background and contour luminance on the hue and brightness of the watercolor effect. *Vision Research*, 144, 9–19. <https://doi.org/10.1016/j.visres.2018.01.003>
- Goldstein, E. B., & Cacciamani, L. (2021). *Sensation and perception (Eleventh)*. Cengage Learning EMEA (UK & Europe).
- Faul, F., Ekroll, V., & Wendt, G. (2008). Color appearance: the limited role of chromatic surround variance in the "gamut expansion effect". *Journal of Vision*, 8(3), 1–20. <https://doi.org/10.1167/8.3.30>
- Friedman, H. S., Zhou, H., & von der Heydt, R. (2003). The coding of uniform colour figures in monkey visual cortex. *The Journal of Physiology*, 548(Pt 2), 593–613.
- Hunt, R. W. G., & Pointer, M. R. (2011). *Measuring colour*. John Wiley & Sons.
- Hunt, D. M., & Carvalho, L. S. (2016). The genetics of color vision and congenital color deficiencies. In *Human Color Vision* (pp. 1-32). Springer, Cham.

- Jasper, H. H. (1958). The ten-twenty electrode system of the International Federation. *Electroencephalogr. Clin. Neurophysiol.*, 10, 370-375.
- Johnson, E. N., Hawken, M. J., & Shapley, R. (2001). The spatial transformation of color in the primary visual cortex of the macaque monkey. *Nature Neuroscience*, 4(4), 409–16.
- Johnson, E. N., Hawken, M. J., & Shapley, R. (2008). The orientation selectivity of color-responsive neurons in macaque v1. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, 28(32), 8096–106.
<https://doi.org/10.1523/JNEUROSCI.1404-08.2008>
- Livingstone, M., & Hubel, D. (1984). Anatomy and physiology of a color system in the primate visual cortex. *The Journal of Neuroscience*, 4(1), 309-356. <https://doi.org/10.1523/JNEUROSCI.04-01-00309.1984>
- Livingstone, M., & Hubel, D. (1988). Segregation of form, color, movement, and depth: Anatomy, physiology, and perception. *Science (American Association for the Advancement of Science)*, 240(4853), 740-749. <https://doi.org/10.1126/science.3283936>
- Nunez, V., Shapley, R. M., & Gordon, J. (2018). Cortical double-opponent cells in color perception: perceptual scaling and chromatic visual evoked potentials. *I-Perception*, 9(1), 2041669517752715–2041669517752715.
<https://doi.org/10.1177/2041669517752715>
- Oostenveld, R., Fries, P., Maris, E., & Schoffelen, J. M. (2011). FieldTrip: open source software for advanced analysis of MEG, EEG, and invasive electrophysiological data. *Computational intelligence and neuroscience*, 2011.
- Pinna, B., Brelstaff, G., & Spillmann, L. (2001). Surface color from boundaries: a new ‘watercolor’ illusion. *Vision Research*, 41(20), 2669–2676.
[https://doi.org/10.1016/S0042-6989\(01\)00105-5](https://doi.org/10.1016/S0042-6989(01)00105-5)
- Pinna, B., & Grossberg, S. (2005). The watercolor illusion and neon color spreading: a unified analysis of new cases and neural mechanisms. *Journal of the Optical Society of America. a, Optics, Image Science, and Vision*, 22(10), 2207–21.

- Rabin, J., Switkes, E., Crognale, M., Schneek, M. E., & Adams, A. J. (1994). Visual evoked potentials in three-dimensional color space: correlates of spatio-chromatic processing. *Vision Research*, 34(20), 2657–2671. [https://doi.org/10.1016/0042-6989\(94\)90222-4](https://doi.org/10.1016/0042-6989(94)90222-4)
- Regan, D. (1989). *Human brain electrophysiology : evoked potentials and evoked magnetic fields in science and medicine*. Elsevier.
- Shapley, R., & Hawken, M. (2002). Neural mechanisms for color perception in the primary visual cortex. *Current Opinion in Neurobiology*, 12(4), 426–432. [https://doi.org/10.1016/S0959-4388\(02\)00349-5](https://doi.org/10.1016/S0959-4388(02)00349-5)
- Shapley, R., & Hawken, M. J. (2011). Color in the cortex: single- and double-opponent cells. *Vision Research*, 51(7), 701–717. <https://doi.org/10.1016/j.visres.2011.02.012>
- Shapley, R., Nunez, V., & Gordon, J. (2019). Cortical double-opponent cells and human color perception. *Current Opinion in Behavioral Sciences*, 30, 1–7. <https://doi.org/10.1016/j.cobeha.2019.04.001>
- Tobimatsu, S., Tomoda, H., & Kato, M. (1995). Parvocellular and magnocellular contributions to visual evoked potentials in humans: stimulation with chromatic and achromatic gratings and apparent motion. *Journal of the Neurological Sciences*, 134(1), 73–82. [https://doi.org/10.1016/0022-510X\(95\)00222-X](https://doi.org/10.1016/0022-510X(95)00222-X)
- von der Heydt, R., Peterhans, E., & Baumgartner, G. (1984). Illusory contours and cortical neuron responses. *Science*, 224(4654), 1260–1262.
- von der Heydt, R., & Pierson, R. (2006). Dissociation of color and figure-ground effects in the watercolor illusion. *Spatial Vision*, 19(2-4), 323–340. <https://doi.org/10.1163/156856806776923416>
- Xing, D., Ouni, A., Chen, S., Sahmoud, H., Gordon, J., & Shapley, R. (2015). Brightness-color interactions in human early visual cortex. *Journal of Neuroscience*, 35(5), 2226–2232. <https://doi.org/10.1523/JNEUROSCI.3740-14.2015>
- Zweig, S., Zurawel, G., Shapley, R., & Slovin, H. (2015). Representation of color surfaces in v1: edge enhancement and unfilled holes. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, 35(35), 12103–15. <https://doi.org/10.1523/JNEUROSCI.1334-15.2015>