Adaptation and Integration of Colour in the Visual System

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Doctor of Philosophy

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Psychology

July 2025

Abstract

Perception of colour is not a static translation from wavelength to hue, but a flexible process which adapts to environmental chromatic properties to maintain stable colour percepts. Colour adaptation has not been well-investigated between a few seconds and multiple days, yet the stability of colour perception despite environmental spectral changes across minutes or hours suggests that adaptation occurs at this timescale. This thesis aims to investigate the properties of this 'medium-term' adaptation, and to localise it within the visual system. Additionally, it aims to investigate colour processing in the brain, primarily whether visual areas process colour monocularly or binocularly.

Chapter 3 investigates the effect of the duration and luminance of adapting environments on changes in colour perception. The results suggest that adaptation to red and blue filters causes shifts in unique hue settings that endure at least five minutes post-adaptation. Both the duration and luminance of filters affected the magnitude of these shifts. Chapter 4 investigates adaptation recovery by comparing hue settings after 60-minutes post-adaptation either in daylight, or in complete darkness. The results show that adaptation aftereffects return to pre-adaptation settings in both conditions, suggesting that colour adaptation recovery is a passive process. Chapter 5 investigates the transfer of adaptation aftereffects between the eyes, by adapting participants to the same colour in both eyes, or different colours in each eye. The results suggest that colour adaptation in one eye does not affect colour settings made with the other eye. Finally, Chapter 5 investigates cortical binocular combination of colour, by recording fMRI while participants viewed LM- or S-cone isolating stimuli in each eye separately, or both eyes together. The results suggest the existence of some populations of monocular colour neurons in ventral stream areas. Altogether, these studies contribute to the wider understanding of the adaptation and combination of chromatic information.

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Acknowledgements

Many, many thanks to my wonderful supervisors, Tony Morland and Heidi Baseler, who have provided me with expert guidance and feedback throughout my PhD, while giving me the independence to follow the research questions that interested me. I have been extremely fortunate to have been so well supported during my PhD. I have enjoyed working with you so much, and I am immensely grateful.

There are many other people without whom I could not have completed the research presented here: thank you in particular to Lauren Welbourne and Joel Martin for the massive amount of help with my fMRI project. Thank you also to Rebecca Lowndes, David Watson, Federico Segala, Bee Quinn, and the YNiC staff for your help, all of which was invaluable. Thank you to Dan Baker for involving me in so many projects which massively helped my development as a researcher. Thank you to my thesis advisory panel, Alex Wade and Karla Evans, who provided me with fantastic advice and suggestions both in and out of our TAP meetings, and who have been so consistently encouraging about and excited by my research. Thank you to Josephine Flockton for listening to me talk through every problem and motivating me onwards. Thank you to Zoha Nadeem and Harper Russell who helped with data collection.

I also have to thank my family, who have stepped up to provide everything from moral support to childcare to enable me to finish my PhD. Thank you to my parents, Shan and Stephen, and to Paul, Becky, and Kathy.

Finally, thank you to the most important people in my life. Connor, I could not have done this without you. On days when I felt like giving up, it was you who kept me going. You have been my greatest supporter and my best friend. Teddy, my beautiful boy, you are the light of my life. I carried you with me through so much of my PhD that the murmurs of the colorimeter must have been some of the first sounds you ever heard. This thesis is dedicated to you.

Author's Declaration

I, Erin Warden-English, declare that this thesis is a presentation of original work, carried out under the supervision of Professor Antony Morland and Dr Heidi Baseler, and I am the sole author. This work has not previously been presented for a degree or other qualification at this University or elsewhere. All sources are acknowledged as references. All the studies contained in this thesis were conducted in accordance with the ethical standards of the Department of Psychology at the University of York and the York Neuroimaging Centre. The data presented in Chapter 5 Experiment 2 was collected as part of an undergraduate research project. The research carried out in Chapter 6 was in collaboration with Dr Joel Martin and Dr Lauren Welbourne.

Data used in this thesis have been presented at the following conferences in the form of talks or poster presentations:

Yorkshire Vision Network, University of York, 26th June 2025. Presentation: "fMRI evidence for monocular processing of colour in visual cortex".

Colour Group Awards Meeting, City University of London, 9th October 2024. Presentation: "Duration and luminance intensity of chromatic environments interact to alter our perception of colour."

46th European Conference of Visual Perception (ECVP), University of Aberdeen, 25th-29th August 2024. Poster session: "Duration and luminance intensity of chromatic environments interact to alter our perception of colour."

Applied Vision Association (AVA) Spring Meeting, University of Plymouth, 17th April 2023. Presentation: "Characteristics of chromatic adaptation to red and blue across four hours".

Chapter 1: Introduction

1.1. Overview

In our perceptual world, colour is not a static property but a dynamic experience. Our visual system interprets the colours of objects in relation to the hues surrounding them, the perceived luminance of the environment, and our visual diet. The radiant energy of light has an influence on the colour we perceive, but there are a range of factors, both physical and cognitive, that interact to determine the sensory experience of colour. Newton famously remarked: "*If at any time I speak of light and rays as coloured or endued with colours, I would be understood to speak not philosophically and properly, but grossly... For the rays to speak properly are not coloured.*" This principle underlies our study of colour perception.

An overview of how light is processed by the visual system is necessary to understand the basis of colour perception. Photons arrive at the eye and are detected by three classes of cone photoreceptor, each optimally tuned to long, medium, and short wavelengths of light (Figure 1.1). (There are also two other types of photoreceptor in the retina: rods, and melanopsin. While these are not generally considered in models of colour vision, there have been suggestions that both rods and melanopsin may influence colour perception to some degree (e.g. Cao et al., 2008; Zele et al., 2018).) Cone photoreceptors are colourblind; they are simply more likely to absorb photons (and therefore fire at a faster rate) at wavelengths to which they are more sensitive. This is known as the principle of univariance, which states that different wavelengths can elicit the same rate of response in a cone type by the alteration of the luminance of the stimulus. For example, a very bright green object may elicit the same response in L cones as a dim red object. Thus, each cone type alone cannot be used to distinguish colours.

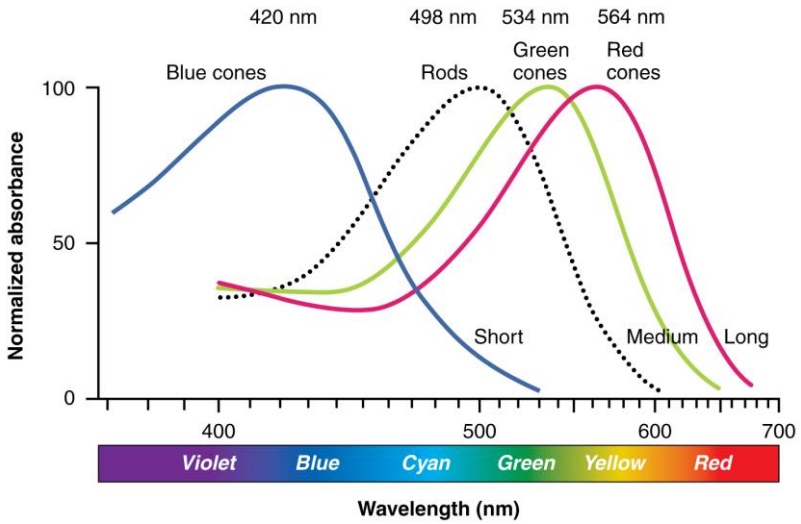


Figure 1.1: *Normalised cone spectral sensitivity functions. From (Bowmaker & Dartnall, 1980).*

The problem posed by the principle of univariance is resolved by comparing the ratios of activity between different cone types. Information from each cone type is decorrelated through recombination in antagonistic retinal ganglion cells, forming three opponent pathways that encode relative differences in the stimulus, rather than absolute stimulus levels. These opponent pathways correspond to L+M, L-M, and S-(L+M), and are each functionally independent. Even after recombination, it is possible for stimuli composed of different wavelengths to elicit the same responses in all three classes of cone; such stimuli are therefore metameric, i.e., seen as the same colour.

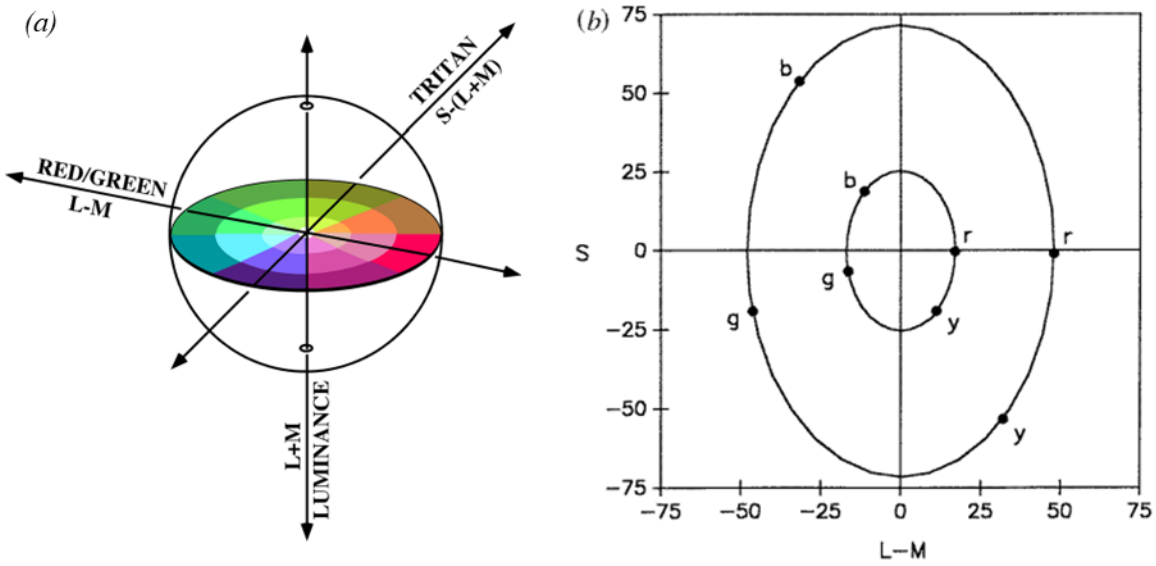


Figure 1.2: *a: Cone opponent pathways represented in DKL colour space. b: Unique hues measured at two different contrasts, plotted as angles along the L-M and S-(L+M) planes within DKL colour space (From Webster, 1996)*

From the retina, this information travels via the optic chiasm to different layers of the lateral geniculate nucleus (LGN) with geniculate opponent cells corresponding to the opponent channels established by the retinal ganglion cells. Colour signals in the LGN are therefore represented along the opponent axes. Many cells in parvocellular layers, and a smaller population of cells in koniocellular layers, have chromatically opponent receptive fields and convey chromatic information to visual cortex.

From the LGN, colour information travels to the primary visual cortex. Unlike in the LGN, where opponent cells are most strongly driven by colours corresponding to the opponent axes, colour-sensitive cells in V1 exhibit preferences for a wide variety of colours (Lennie et al., 1990), suggesting that the visual cortex again recombines the information (although there is some suggestion that colour preferences of V1 cells do cluster around the opponent axes; Brouwer & Heeger, 2009). Cells in the visual cortex are defined as being colour-sensitive if they difference L-, M-, or S-cone stimulation rather than summing it, allowing them to respond to isoluminant changes in hue (Gegenfurtner, 2003). According to traditional estimates, around 50% of neurons in the visual cortex are sensitive to colour. However, it is now known that many cells respond weakly to both luminance or colour, and that there is a continuum of cells with preferences for changes in luminance or changes in colour.

Within V1, colour-sensitive cells are often found within cytochrome oxidase ‘blobs’, at the centre of ocular dominance columns (Chatterjee et al., 2021). These cells tend to respond most strongly to uniform surfaces of their preferred colour. Colour-sensitive cells found outside blobs may respond preferentially to combinations of colour and pattern, responding only weakly to colour if no spatial component is present in the stimulus (Yoshioka & Dow, 1996).

From the primary visual cortex, information is relayed outwards to V2, V3, and later visual areas, into the temporal and parietal lobes. ‘Visual areas’ in this context refers to regions of the brain that respond to visual stimuli and have a broadly retinotopic organisation. While most visual areas beyond V1 and V2 respond to colour, the post-striate areas that respond most to colour are V4, VO1 and VO2 (Mullen, 2019). These areas are situated on the ventral surface of the brain, and are collectively referred to as the ‘ventral stream’ of visual perception, which is thought to encode information pertaining to shapes and object recognition (Milner, 2001). Initially, area V4 was highlighted as being particularly sensitive to chromatic stimuli (McKeefry & Zeki, 1997a), but later fMRI evidence suggested that there was a distinct area adjacent to V4 with clear colour selectivity (Hadjikhani et al., 1998). This area was initially termed ‘V8’, but subsequent retinotopic mapping defined it as two areas, now usually referred to as ‘VO1’ and ‘VO2’.

Colour opponency theoretically resolves ambiguity in colour appearance resulting from the univariant outputs of cones. However, there are many situations in which the same wavelengths may appear different colours, or different wavelengths may appear to be the same colour. For example, an orange may still be perceived as orange in colour even under very large changes in illumination, meaning completely different wavelength spectra are reflected from its surface. To preserve colour constancy, the visual system is able to discount the illuminant in many situations to infer colours from local comparisons within a scene (Werner, 2014). It can also adapt to global changes in illumination in order to maintain the an accurate perception of the world, restoring a ‘normal’ appearance even after extreme changes in the spectral qualities of the environment (Tregillus & Engel, 2019). Rather than being a static translation of the wavelengths in our environment, our colour perception is a dynamic interpretation of the world around us.

Previous studies have suggested that adaptation involves two distinct mechanisms: a rapid, short-term mechanism that maintains consistency across a scene, and a long-term mechanism that shifts the baseline of our perceptual expectations and lasts for hours or days. These concurrent mechanisms of adaptation have been observed after viewing various types of visual information, such as orientation, colour, contrast, or spatial frequency (Zhang et al., 2009; Haak et al., 2014; Tregillus & Engel, 2019). Fast adaptive mechanisms can be shown through immediate visual aftereffects, for example, viewing a grating tilted at a certain orientation for a few seconds can bias the perceived orientation of gratings viewed immediately afterwards (Blakemore & Nachmias, 1971), suggesting rapid adaptation of neurons to the observed orientation. However, eliciting changes in threshold sensitivity to vertical or horizontal orientations requires longer exposure. Zhang et al. (2009) found that one hour of adaptation was insufficient to produce threshold shifts; significant changes only emerged after four hours, indicating a slower adaptation process. This pattern - a rapid adjustment followed by long-term normalisation - in response to changes in the environment may reflect a general principle of adult neuroplasticity throughout the visual system, from the retina through to higher-level visual areas (Haak et al., 2015).

The purpose of colour adaptation appears to be the maintenance of stable colour percepts, regardless of changes in mean illumination of the environment. It has been observed that following shifts in the mean chromaticity of the environment, the perceived colours of objects gradually return to their original appearance. This has been seen both in long-term adaptation studies that manipulate the chromatic environment (Kohler, 1963; Neitz et al., 2002; Belmore & Shevell, 2008), in naturalistic experiments on the effect of cataract yellowing on colour perception (Delahunt et al., 2004; Tregillus et al., 2016) or seasonal changes in hue judgements (Welbourne et al., 2015).

Many elements of adaptation remain unexplored. The timescale of long-term adaptation is still unclear, largely due to variability across different participants and experimental designs. While mechanisms of long-term adaptation have been proposed, many predictions of these models remain untested. The locus within the

visual system of long-term adaptation is still a topic of ongoing debate. This introduction will review our current understanding of colour adaptation, focusing primarily on long-term adaptation, while also addressing short-term processes. It will discuss key experiments that have investigated long-term adaptation, explore proposed mechanisms underlying this process, and consider the roles of different cone types, as well as the dynamics of adaptation recovery. Finally, it will evaluate evidence concerning binocular integration of colour information.

1.2. Short term colour adaptation

Short-term adaptation to colour occurs over a timescale ranging from a few milliseconds to several minutes. The majority (50-60%) of this adaptation occurs virtually instantaneously, with the remaining adaptation occurring over a time course of seconds to minutes, reaching completion by about 2 minutes of exposure to the adapting stimulus (Rinner & Gegenfurtner, 2000). While the traditional view of short-term adaptation holds that it is driven by adaptation in retinal cells, either the photoreceptors, or retinal ganglion cells, other studies have proposed the involvement of multiple mechanisms at later stages of the visual system (Kuriki & MacLeod, 1997). However, the canonical view of short-term adaptation remains that it is attributable to retinal processes, and that it is characterised by both rapid saturation and rapid decay.

Jameson and Hurvich (Jameson et al., 1979) suggested two distinct processes of short-term adaptation (defined in their study as an adaptation period of up to 10 minutes). The first process involves reweighting the sensitivity of the different cone types, while the second involves altering the equilibrium point of red/green channels at an opponent neural site, and is only engaged after longer or repetitive doses of a stimulus. The first mechanism aligns with the principles of von Kries adaptation, which posits that light adaptation occurs independently within each cone class before opponent recombination. Therefore, adaptation scales cone sensitivities to a constant scaling factor that maintains a constant mean response in each cone type (von Kries, 1905). For example, a red light might elicit a greater response in L cones

than M cones, but L cones would also undergo a larger adaptation, leading to a greater suppression of the responsiveness of L cones compared to M cones. This reweighting of sensitivity (in cones or cells in later visual areas) is often referred to as 'gain control'. The majority of adaptation to the illumination of an environment occurs as a result of von Kries adaptation (Brainard & Wandell, 1992). The second of these mechanisms corresponds to contrast adaptation, in which sensitivity changes occur in pathways that are tuned to specific stimulus properties, such as colour, orientation, or movement. In terms of colour, this represents an adaptation along opponent channels. This form of adaptation is generally thought to occur at a cortical locus (Webster, 1996). Adaptation along the chromatic contrast axes over 180 seconds is selective for temporal frequency, spatial frequency, and orientation, which is inconsistent with a cone-specific locus of adaptation (Webster & Mollon, 1994). However, some evidence that is generally used to identify cortical adaptation (such as interocular transfer) has not been found to be present in colour adaptation in many studies (though this is controversial – see section 1.6.1).

Rinner & Gegenfurtner (2000) proposed that short-term adaptation (defined in their paper as an adaptation duration of up to 120 seconds) occurs at three timescales. In their experiment participants were adapted to a uniform background of red, green, yellow, or blue. Increment thresholds along the red-green or blue-yellow axes, or colour appearance as determined by achromatic matching, were measured at adaptation durations from 25 milliseconds and 121 seconds. Based on the temporal profiles of the responses, three mechanisms of adaptation were identified: a slow process with a half-life of approximately 20 seconds, a fast process with a half-life of 40-70 milliseconds, and an instantaneous process with a half-life of under 10 milliseconds. The majority of the change in colour appearance (over 50%), was explained by the instantaneous mechanism. The authors speculate that this process occurs at a cortical level, and can be explained by multiplicative gain control. They further suggest that even stimulation that lasts for under a second can induce adaptive changes at a cortical level. This view of short-term colour adaptation challenges previous assumptions that due to the rapidity of short-term adaptation and its recovery, colour adaptation was solely a retinal function.

Through these adaptive processes, the visual system rapidly collects information about contrast and luminance to adjust neural sensitivity at multiple levels, up- or down-weighting cone signals in order to maintain an optimised representation of the chromatic environment. It is reasonable to assume that this information is also available to mechanisms involved in long-term chromatic adaptation, whether or not it is directly used. For example, if estimates of the mean chromaticity of an environment are computed on a very rapid scale, it is physiologically plausible that they may also be integrated in longer-term mechanisms that track mean chromaticity over extended periods.

1.3. Long term colour adaptation

Long-term colour adaptation is defined here as the shifts in hue perception that occur after an observer is exposed to a chromatically altered environment for hours, days, or weeks at a time. The first question to consider is whether it is genuinely distinct from short-term colour adaptation, or a continuation of the same underlying process. One possibility is that even prolonged changes in colour appearance might be explained by rapid adaptation mechanisms at the level of the photoreceptors, especially if those mechanisms are repeatedly engaged. Alternatively, both long and short-term processes could engage the same cortical mechanisms. However, evidence from the persistence of perceptual changes after long-term adaptation, and the functional independence observed between short- and long-term adaptation in some studies, suggests that these two forms of adaptation rely on distinct mechanisms.

As noted by Tregillus & Engel (2019), although altering the chromatic environment of a participant is a straightforward manipulation, only a handful of multi-day experiments have been conducted. The earliest recorded investigation of long-term colour adaptation was a single-observer study performed by Kohler (1963), who qualitatively reported that the longer one spent in a colour-altered environment, the more the world regained its normal appearance. The first quantitative study of the effects of long-term colour adaptation was performed by Eisner & Enoch (1982), who monocularly adapted participants using a red filter worn continuously over the course of a week. Their results showed that measurements of unique yellow (a point on the

spectrum where a stimulus appears neither more green nor more red) shifted towards longer wavelengths after red adaptation, and that this effect persisted for hours or days after adaptation within the adapted eye. Participants were not impaired on tests of colour matching or colour blindness, suggesting the effects could not be attributed to optical changes in the eye. The authors concluded that the changes in the appearance of the world were due to a post-receptoral mechanism of chromatic adaptation, primarily based on the long duration of the effect, which exceeded the timescale of known photoreceptor adaptation.

The idea that long-term colour adaptation may reflect a cortical "renormalisation" mechanism was introduced by Neitz et al. (2002). Their study aimed to determine whether visual experience simply reinforces a fixed, innate encoding of colour, or whether it actively shapes colour perception over time. To investigate this, Neitz *et al.* measured the L:M cone ratio in the retinas of 32 participants and compared these ratios to each participant's unique yellow settings. Despite substantial variability in the proportion of L to M cones across individuals, they found surprisingly little variation in colour appearance. This suggested the existence of a compensatory mechanism that adjusts for individual differences in cone distributions by normalising the relative weightings of cone signals. The authors proposed that this system may use the average illuminant of an environment as the equilibrium point for the red/green chromatic channel, acting as a base around which to detect other colours. Therefore, changes in the mean chromaticity of the visual world could trigger a cortical renormalisation of the red/green colour system, leading to altered colour percepts. This would explain how the visual system maintains perceptual stability over long periods of time.

This proposed renormalisation mechanism predicts that after prolonged exposure to a chromatic environment biased towards one part of the visible spectrum, the internal 'equilibrium' point of the red/green channel should become biased in the same direction. For example, if the observer viewed an environment dominated by long-wavelength (red) light, the average illuminant would be biased towards red. As a result, the baseline equilibrium point should be recalibrated, and greater amounts of red light would subsequently be required for a stimulus to appear subjectively unchanged. In other words, if all "red" signals are dampened due to adaptation to red

light, then post-adaptation stimuli would need to contain more red to elicit the same percept as before, in order to compensate for the suppressed sensitivity of the 'red' mechanism. This shift reflects an adaptive compensation for the altered mean chromaticity of the environment.

To test their renormalisation hypothesis, Neitz et al. (2002) adapted participants to red and green light, for 4-12 hours per day, over the course of 8-25 days. It was found that shifts in unique yellow settings increased progressively across the adaptation period, regardless of the total duration, and persisted for several days afterwards (see Figure 1.3 for the results from one participant). There were large individual differences in the magnitude of the shift between participants, but this was attributed to the differences in adaptation methods and daily exposure durations. The researchers interpret these results as evidence for a long-term normalisation mechanism which causes an enduring change in the weighting of cone responses in chromatic channels at a cortical level.

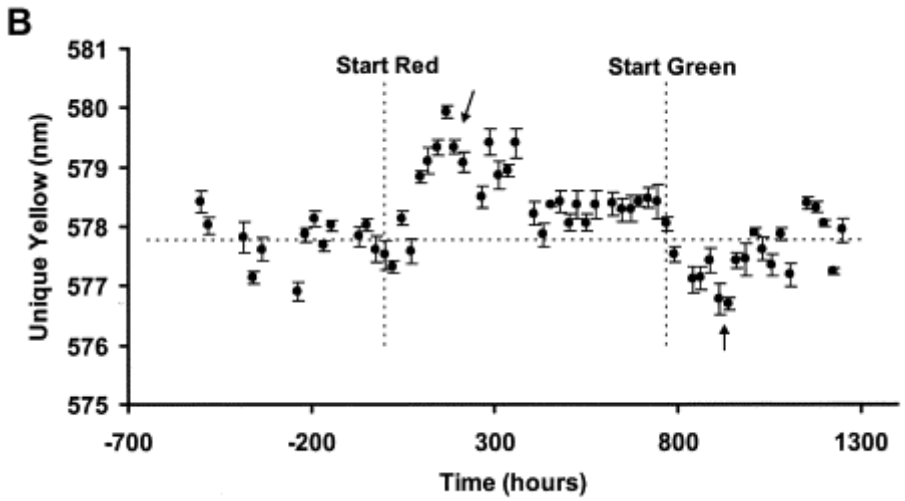


Figure 1.3: *Unique yellow settings for one participant, adapted for 12 hours/day using coloured contact lenses. Dashed lines indicate when the adaptation period began; arrows indicate when it ended. Settings for unique yellow can be seen to shift towards longer wavelengths following adaptation to red, and towards shorter wavelengths following adaptation to green. From Neitz et al. (2002).*

Neitz *et al.* suggest renormalisation occurs by a gain control mechanism that adjusts the weighting of each cone type according to the chromatic environment. For example, in a predominantly red environment, L-cones would be down-weighted,

while S-cones may be up-weighted, in order to suppress the relative influence of L-cone signals on perception. However, subsequent work by Belmore & Shevell, (2008) has suggested that any post-retinal normalisation mechanism of cone reweighting cannot rely solely on a linear multiplicative gain factor for each cone type. In their study, three observers were adapted to long wavelengths of light for 1 hour per day for 12-14 days, then asked to set unique yellow through an additive mixture of two wavelengths, instead of adjusting a single wavelength along the spectrum to locate unique yellow (as in Neitz *et al*.'s study). A fixed intensity light at 540nm was combined with an adjustable intensity light at 660nm to create the test stimulus. As predicted, following adaptation to a red environment, a higher intensity of the 660 nm light was required to create unique yellow. However, this effect was not linearly proportional to the intensity of the 540 nm light. When the luminosity of the 540nm light was low, a disproportionally greater luminous intensity of the 660nm light was needed to produce unique yellow after adaptation compared to when the luminosity of the 540nm light was higher (see Figure 1.4).

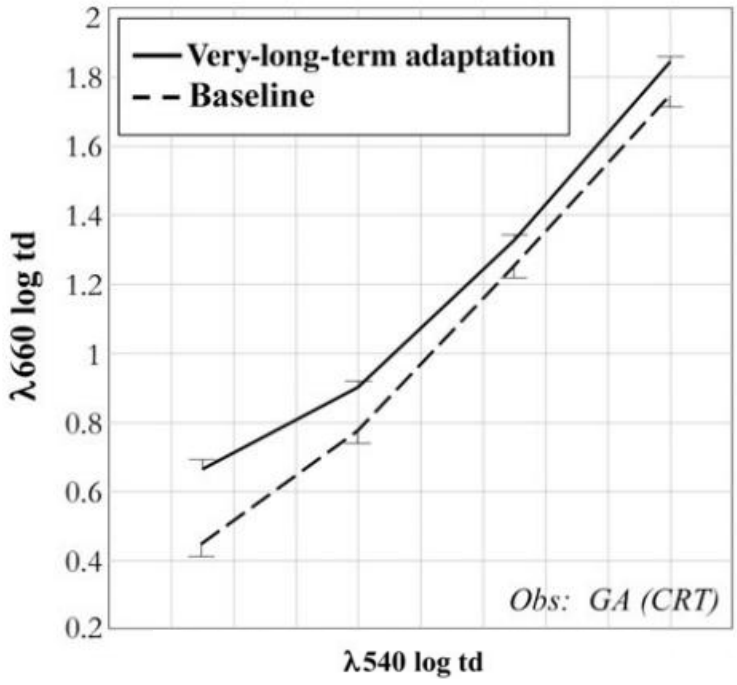


Figure 1.4: *Amount of 660nm light needed to be added to the mixture in order to form unique yellow, as a function of the intensity of the 540nm light (on the horizontal axis), at baseline and following adaptation to red, for one participant. A larger difference in the amount of 660nm light needed between the baseline and adapted conditions can be seen when the intensity of the 540nm light is low. From Belmore and Shevell (2008).*

If there were simply a single multiplicative gain factor for each cone class, there should be a constant change in the shift in luminous intensity chosen for the 660nm light in the unique yellow mixture. This non-linearity suggests that cone reweighting during long-term adaptation cannot be fully accounted for by a simple linear gain control model.

Compelling evidence for long-term colour adaptation as a separate mechanism to short-term adaptation comes from studies demonstrating the additivity of the two mechanisms. Belmore & Shevell (2011) observed that while both long- and short-term adaptation induce shifts in unique yellow, short-term adaptation produces larger, more transient shifts that saturate rapidly. They reasoned that if both forms of adaptation rely on the same underlying mechanisms, then shifts in unique yellow should never be larger than the saturation point of short-term adaptation. Conversely, if the effect of long-term adaptation is cumulative with the effect of short-term adaptation, this implies they arise from separate mechanisms. To test this, participants were adapted to a red grating for 1 hour per day over the course of 12-14 days. Participants' unique yellow measurements were recorded 22 hours after each session. After recording their initial post-adaptation unique yellow, participants were then adapted for a further 3 minutes to a red stimulus, and their unique yellow recorded again, with top-up exposure to the adapting stimulus. The results showed that the shift caused by short-term adaptation occurred in addition to the long-term shift, and the magnitude of long-term adaptation was unaffected by the presence of short-term adaptation. This additive pattern supports the existence of independent and concurrent mechanisms for short- and long-term colour adaptation.

Despite this evidence, the existence of long-term colour adaptation as a distinct mechanism remains contested. Some researchers have criticised the findings and methodologies used by long-term colour adaptation research. For example, Eskew & Richters (2008), found that after adapting observers to red lenses, unique yellow settings were much more variable than those reported in previous studies. Furthermore, after the adaptation period was over, observers never returned to their baseline unique yellow measurements, despite long recovery periods. They suggest that this is evidence that the change in unique yellow settings in previous studies was a spurious result, potentially driven by the use of non-naïve participants. Li et al.,

(2020) attribute this variability to a lack of contextual information in the test environment, with measurements relying on isolated colour stimuli in dark rooms. They argue that when adaptation occurs, we do not just learn to adapt to the colour-altered environment for an isolated period of time, but that we are able to retain a record of the altered chromatic environment and switch more quickly back to the adapted state following reintroduction to the same colour-filtered environment. Observers may use contextual cues to trigger switches in adaptation state. The absence of contextual cues in testing, such as visual information about ambient lighting or scene structure, may hinder the visual system's ability to select the appropriate adaptive state, thereby increasing variability in results.

It is also important to recognise that significant differences in timings and techniques are used between, and sometimes within, studies. Chromatic filtering may be achieved with coloured goggles, coloured contact lenses, or filtered lighting in a room, each of which may influence adaptive processes slightly differently. Furthermore, the duration of daily exposure varies widely (from as little as one hour to nearly full-time wear) and total adaptation periods range from 5 to 24 consecutive days. This methodological diversity presents a challenge for drawing direct comparisons across studies or for establishing a definitive timescale over which long-term adaptation occurs. Without standardisation of exposure conditions, it remains difficult to determine how generalisable the observed effects are, or whether disparate findings reflect true differences in adaptation or artefacts of experimental design.

1.3.1. Naturalistic long-term colour adaptation

Long-term colour adaptation is also observed in the natural world, and is not confined to the laboratory. This phenomenon likely serves an important function in maintaining perceptual constancy amid gradual changes in the visual environment, such as seasonal shifts in mean chromaticity or age-related changes to the eye's optics.

In one example of this, Neitz et al. (2002) tested the unique yellow settings of deuteranomalous men, and also used molecular genetics to infer the absorption spectrum of their abnormal M-cones. They calculated that, according to their theory of a gain control mechanism, these participants' unique yellow settings aligned with reweighted cone signals that differed from those of typical trichromats. They suggest deuteranomalous individuals undergo long-term adaptation in order to compensate for their altered photoreceptor sensitivities (the idea that adaptation may compensate for colour vision deficiency has been further developed by modelling work by Webster et al., 2010). Neitz *et al.* concluded that the proposed gain control mechanism must be fully adjustable to any value, given sufficient time to adapt.

It is not only colour-anomalous individuals whose visual systems are constantly adapting. Over the course of a lifetime, the lens of the eye yellows, absorbing more, and therefore transmitting less, short wavelength light as age increases (Pokorny et al., 1987). This should cause the world to look increasingly yellow, as the lens absorbs gradually less light at shorter wavelengths, yet chromatic judgments are very stable across the lifespan (J. S. Werner & Schefrin, 1993). This implies long-term adaptation processes are being utilised to constantly recalibrate the interpretation of chromatic input in the face of physiological change.

This ability to adapt to changes in the absorption spectrum of the eye across a lifespan has been demonstrated following cataract surgery. Delahunt et al. (2004) measured white point settings (in which observers must alter a field such that it appears achromatic) for individuals before and after cataract removal surgery. Following surgery there was a large increase in the amount of short-wavelength light reaching the retina. Immediately post-surgery, participants' white point settings shifted towards 'bluer' settings. Over several months, achromatic settings gradually returned to similar settings as before the surgery, implying a very slow, long-term, adaptive process.

Tregillus et al. (2016) tested a similar effect in the opposite direction. Younger participants adapted over 5 days to yellow contact lenses that mimicked the absorption of the lens of a 70-year-old. A large shift in white point settings was found at the start of the day (when the lens was first donned), but this effect weakened

over the course of the day, suggesting adaptation to the lens. However, no persistent effect was found when the lenses were removed, and adaptation was not found to strengthen over the course of multiple days. The authors suggest that there are multiple mechanisms for long-term adaptation; that there is a 'medium term' adaptation that occurs over the course of several hours, which is perhaps separate to the very long-term adaptation that occurs over weeks or months. It may be that smaller shifts in the chromatic environment require longer periods of time to induce persistent adaptation effects, while larger shifts in the environment (such as in the experimental manipulations described above) engage long-term changes more readily.

Long-term adaptation can also occur naturally without any changes to ocular physiology. Welbourne et al. (2015) demonstrated that the wavelength chosen by observers to represent unique yellow varies seasonally, with shorter wavelengths being chosen in the summer, and longer wavelengths being chosen in the winter. They suggest that this difference may be driven by changes in the mean chromaticity of the environment, with more green wavelengths being reflected in summer than winter due to an increase in vegetation. This further supports the idea of a flexible process of renormalisation that is dependent on the chromatic environment.

This naturalistic evidence further supports the existence of long-term adaptation, suggesting a biological incentive for an adaptive mechanism that operates on a much longer timescale to short-term adaptation. The evidence also suggests that the timescale of long-term colour adaptation can be as long as weeks or months, far longer than retinal adaptation, again implying the independence of long-term and short-term adaptation processes. However, some inconsistency remains between naturalistic and laboratory data regarding the duration and persistence of colour aftereffects following long-term adaptation.

1.3.2. The roles of different cone pathways in long term adaptation

A notable gap in the literature is consideration of the role of S-cone pathways in long-term adaptation. Much research focuses on defining adaptation as the equilibrium between the L- and M- cone responses, with gain-control models

typically referring to gain control of the L-M axis. However, some research does suggest that the S-cone pathway is also able to adapt to the chromatic environment. Hammond (2008) measured S-cone sensitivity and yellow-blue cancellation functions (which involve measuring the amount of yellow required to be added to blue to create a 'pure' green), and found these functions remained consistent across the retina, regardless of large differences in macular pigment density. Given that macular pigment selectively absorbs short-wavelength light (with peak absorption around 460nm), this consistency implies the presence of a compensatory long-term adaptation mechanism along the yellow–blue axis. Whether this system of adaptation uses the same normalisation mechanism as the proposed L:M cone normalisation system has not yet been considered. It might be expected that adaptation of the S/(L+M) pathway works similarly to adaptation of the L/M pathway, but given key differences in architecture (such as the relative sparsity of S-cones, the distribution of ganglion cells encoding the S-cone signal, and distinct cortical projection sites), this cannot be assumed.

1.4. Adaptation between short and long timescales

Few studies have investigated adaptation on a timescale between a few minutes and multiple days. Shimakura & Sakata (2022) investigated chromatic adaptation when participants were adapted continuously to yellow light in their peripheral retina for up to 70 minutes, and their neutral point settings tested in the fovea. Firstly, they showed that participants' neutral point settings did shift in the fovea after only peripheral adaptation, suggesting that adaptation does occur at post-receptoral levels of processing. The authors suggest that this is indicative of adaptation occurring at a cortical level, as they suggest complex neural mechanisms are necessary for integrating information across the central and peripheral retina. Secondly, they observed that neutral point settings began to shift after just a few minutes of adaptation (within 10 minutes), but this shift then plateaued and gradually reversed between 20 and 60 minutes of continued exposure. This suggested that perhaps a short-term mechanism of adaptation was becoming saturated, while long term mechanisms were either not being engaged, or not building up over time. The authors suggest that the results may be indicative of an internal representation of daylight illumination, which resists recalibration after shifts in the chromatic

environment, enabling us to estimate it even when placed in colour-altered environments.

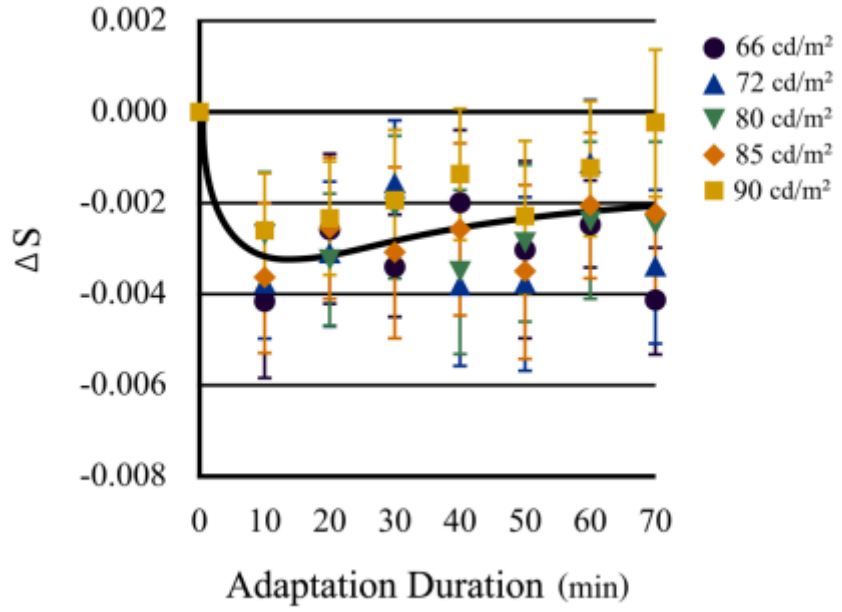


Figure 1.5: *Shifts in neutral point setting along the blue-yellow axis in the fovea after 0-70 minutes of peripheral adaptation to yellow. From Shikamura and Sakata (2022).*

Li et al. (2020) also conducted a study in which participants were adapted to red goggles in 1-hour intervals across the course of five days, and their unique yellow settings measured both while they were wearing the goggles, and after the goggles had been removed. They found that participants were consistent in the amount to which they adapted to the goggles after one hour of adaptation, averaging about 13 degrees of hue angle per hour. Adaptation increased steadily throughout the 60-minute exposure period without reaching a plateau, indicating that the active mechanism had not yet saturated at the point the glasses were removed. This would suggest that the adaptation mechanism being engaged was able to continue adapting for at least 60 minutes. They also found that the repeated exposure to the red environment did not alter the rate of adaptation decay. Once the goggles were removed, adaptation effects decayed exponentially and returned to baseline within approximately 30 minutes. These results suggest that the adaptation observed within the hour reflects a short-term process that can continue accumulating over medium durations, without transitioning into a persistent, long-term state. However, the researchers also found evidence of a gradual shift in baseline settings across the

five days, again supporting the view that short- and long-term adaptation processes can operate concurrently.

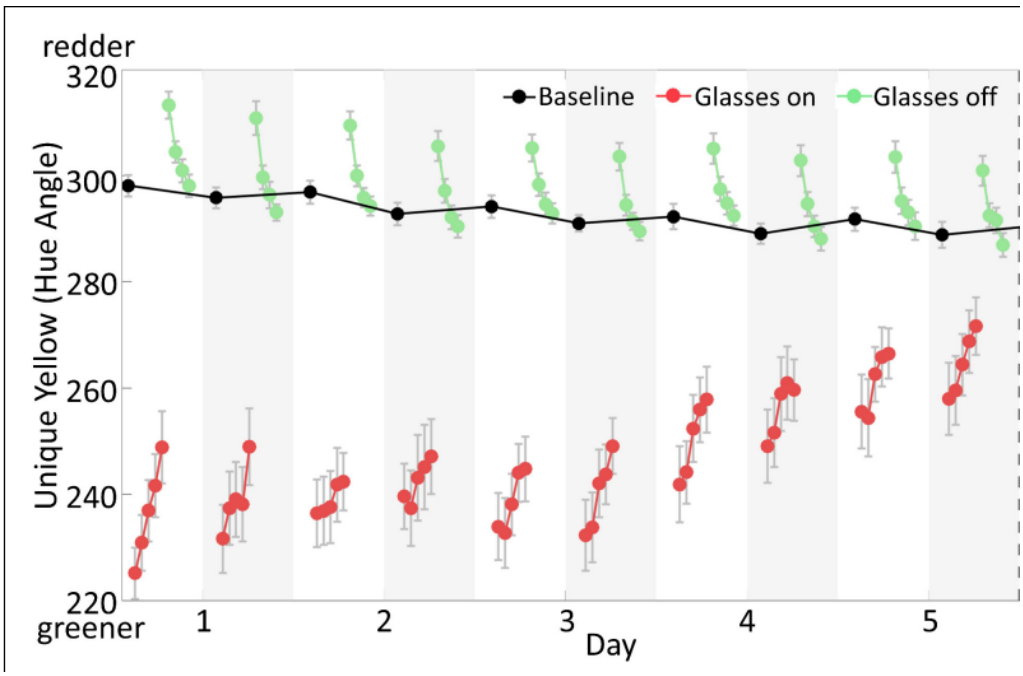


Figure 1.6: *Adaptation to red goggles increases across the course of an hour (red dots), and decays back to baseline after half an hour without goggles (green dots). The baseline (black dots) shows a small but significant shift across days. From Li et al (2020).*

Together with Shimakura and Sakata (2022), these findings suggest that adaptation in the 10–60-minute window may represent a temporal zone in which short-term mechanisms persist, accumulate, or even interact with slower, longer-term recalibration processes.

1.5. Adaptation Recovery

In short-term adaptation, recovery is a rapid process, as evidenced by visual aftereffects which fade after only a few seconds. The recovery of cone photoreceptor sensitivity after photoreceptor bleaching (in which cones are exposed to very bright, saturating stimuli) is well-characterised, with full recovery taking 2-4 minutes (Hecht et al., 1937; Mahroo & Lamb, 2004). In retinal ganglion cells, Yeh *et al.* (1996) demonstrated that adaptation to brief chromatic changes return to baseline within 5–30 seconds, with the recovery rate depending on the specific visual stimuli presented during the recovery period. This evidence supports the interpretation that the retina

encodes fast, reversible adaptation, consistent with the transient nature of short-term colour aftereffects.

Wright (1946) showed that the recovery of adaptation depends on its magnitude; after adaptation to a red light, green and red sensitivity recovery takes longer when the magnitude of the initial change in sensitivity is larger. Jameson et al. (1979) show that five minutes of adaptation produces perceptual shifts that recover within five minutes of exposure to normal illumination, suggesting that short-term adaptation recovers over a similar timescale to its induction. However, they also found that that rate of adaptation recovery could be attenuated by alternating the adapting stimulus with periods of darkness. In their experiment, participants were either adapted to a stimulus at 540nm or 620nm, with exposure delivered either continuously for five minutes, or alternated with 10-second intervals of darkness over 10 minutes. Although the alternating condition produced smaller shifts in unique yellow settings, the shifts lasted for slightly longer than in the continuous exposure condition, suggesting that the rate of recovery is not linearly related to the magnitude of the initial shift. The rate of recovery can also be slowed by using complex stimuli. For example, the McCullough effect (a colour-contingent orientation aftereffect) is famously long-lasting, and can persist for 24 hours after only 20 minutes of exposure (Howard & Webster, 2011). This unusually long duration is thought to result from the involvement of cortical mechanisms in encoding orientation and colour associations, in contrast to the primarily retinal locus of standard short-term chromatic adaptation.

In long-term adaptation, Neitz et al. (2002) showed that the changes induced by long-term exposure to a chromatically altered environment persist for days or weeks back in normal illumination. Similarly, Delahunt et al. (2004) show that after cataract surgery, it can take months for colour perception to return to pre-surgery levels. However, the mechanisms for this de-adaptive process have not been explored. According to Neitz's renormalisation theory, long-term adaptation involves an alteration of the null point in the L/M ratio in the visual cortex. If adaptation is cortical, it can be inferred that adaptation recovery must also be cortical. It has been suggested that cortical adaptation may need active input in order to de-adapt. For example, one explanation of the longevity of the McCullough effect is the rarity of de-adapting stimuli in day-to-day life; we do not see many stripy coloured objects that

would provide active input to alter the existing adaptation to coloured stripes (Vul et al., 2008). Discovering whether adaptation recovery is active (requiring visual input to de-adapt) or passive (returning to baseline regardless of visual input) would have implications for the locus of long-term adaptation, as well as for Neitz's theory of renormalisation.

1.6. Adaptation throughout the visual system

Adaptation occurs at multiple levels of the visual system. Information about global changes to the chromatic environment must be relayed from early stages to later ones, with adaptation signals potentially repeated and refined at each successive level. It is plausible that adaptation at each of these loci is engaged after different amounts of exposure to a chromatically-altered environment. For example, very short-term adaptation of the photoreceptors may not cause adaptation later in the visual system, but when the effect is prolonged by an enduring change in the visual environment, this may cause adaptation in retinal ganglion cells, cells in the LGN, or in the cortex.

The idea has been proposed before that multiple populations of cells may adapt in different ways and at distinct timescales in order to optimise perception according to the duration of exposure to a given visual environment. Haak *et al.* (2014) show that adaptation to visual contrast over four days peaks around 1-2 days into the adaptive period, then declines, then slowly increases again. They suggest that separate populations of neurons may adapt on different timescales, with a computationally expensive rapid response being initially engaged, then declining with prolonged exposure to the adapting stimulus as the costs to remaining adapted begin to outweigh the benefits. At this point, a slower but more robust adaptation response is engaged, adjusting neural codes to represent visual contrast more accurately. Bao *et al.* (2013) similarly argue that contrast adaptation is governed by multiple mechanisms operating along a continuum of timescales. This may reflect an optimal strategy, as multiple variations to the environment at different timescales can occur simultaneously (Kording et al., 2007). For example, the visual system must adapt to short-term chromatic changes while still maintaining a state of long-term adaptation

(Belmore & Shevell, 2011). In order to be able to optimally discriminate colour, we must therefore be able to adapt simultaneously at a range of timescales.

One explanation for how adaptation works at multiple stages of the visual system could be that similar adaptation signals are passed forward through successive stages. For example, colour adaptation could cause gain control alterations of different cone types in retinal ganglion cells, then this gain control factor could be propagated along visual pathways to the LGN, and then to the visual cortex, which similarly recalibrate opponent pathways using the same gain control factor. In this model, the further along the pathway the signal travels, the longer the adaptation effect might persist. However, this explanation does not take into account that different stages of the visual system receive different information. For example, it has been suggested that a second recombination of cone signals may occur in the visual cortex. The information being received by later visual areas such as V4 is therefore very different to the information received by the LGN. Furthermore, there is a greater representation of S-cone-sensitive signals in post-V1 visual areas in macaques, suggesting that there may be a retransformation of cone signals away from cone opponency, or an amplification of the signals from certain pathways above others (Du et al., 2022a).

Another factor that affects the information available at each stage of the visual system is the binocular integration of colour. Some stages of the visual system will have binocular input, and some stages will only have monocular input. As it is possible for each eye to adapt independently (Delahunt et al., 2004), the visual system must sometimes be required to integrate disparate adaptive information from each eye. Given these differences in input and organisation across the visual hierarchy, it seems unlikely that adaptation simply propagates forward unchanged from the retina. Instead, each stage may recalibrate its response based on both inherited and locally available information, enabling more efficient and context-sensitive adaptation.

1.7. Binocular integration of colour in the cortex

It is well-established in the neuroimaging literature that most early visual areas respond to colour (Mullen, 2019). Each visual area consists of a retinotopic map which responds selectively to its preferred stimulus features. Area V1 responds to colour, as well as to achromatic spatial information including orientation and spatial frequency. Further along the ventral surface, area V4 has been shown to be extremely responsive to coloured stimuli (McKeefry & Zeki, 1997b; Mullen, 2019). Continuing along the ventral stream, fMRI evidence suggests there are high colour responses in the ventral occipital areas, which are distinct from V4, and have the strongest response to colour of the extrastriate areas (Brewer et al., 2005; Mullen et al., 2007). Originally identified as a separate, colour-specialised area adjacent to V3v, named V8 (Hadjikhani et al., 1998), this area has now been retinotopically characterised as two areas, now generally referred to as VO1 and VO2, which represent the entire contralateral hemifield (Arcaro et al., 2009; Wade et al., 2002), and respond strongly to colour (Brewer et al., 2005). It has therefore been suggested that one of the functions of the ventral stream of visual processing may be to process colour information.

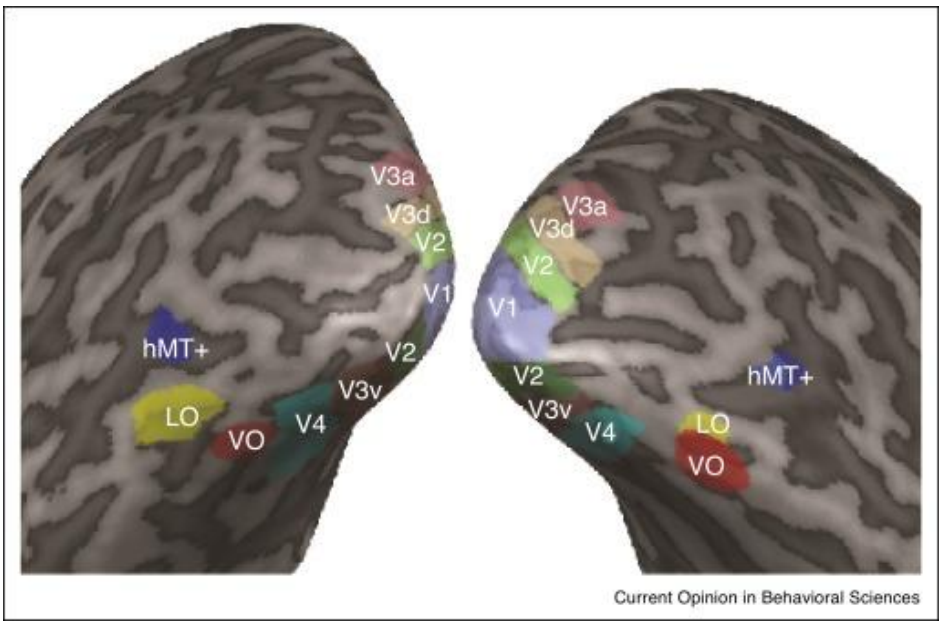


Figure 1.7: *Visual regions labelled on inflated brain surface. From Mullen (2019)*

Colour processing regions are, like most other post-V1 visual areas, assumed to be binocular. The classic model of binocular integration posits that information is combined between the eyes in V1, so that downstream areas receive information

that is already integrated between the eyes. This is largely influenced by the pioneering work of Hubel and Wiesel (Hubel & Wiesel, 1962), who suggested that around 84% of neurons in cat V1 respond to stimuli presented to either eye. Later work has corroborated this finding, with the proportion of binocular neurons in V1 in macaques being estimated at around 78% (Dougherty et al., 2019). However, monocular neurons do still exist in V1, largely within layer 4c. These are generally, but not always, organised into ocular dominance columns based on the eye preference of the neuron (Adams & Horton, 2006). Colour-sensitive neurons are primarily found within cytochrome oxidase 'blobs' at the centre of ocular dominance columns (Chatterjee et al., 2021). This has led to the suggestion that monocular neurons in V1 may preferentially process colour, and that therefore separate monocular pathways for colour are maintained in V1. While there is now considerable data to suggest that colour cannot be solely processed by monocular pathways in V1 (e.g. Peirce et al., 2008), there may still be some monocular representation of colour remaining in V1, particularly for low-spatial frequency chromatic stimuli.

In V2 and V3, there is also some evidence that colour may be processed in separate pathways, though there is little evidence that these pathways are distinctly monocular. Ocular dominance columns in V1 project to 'thin stripe' layers of V2 in non-human primates (Tootell et al., 1983). There is evidence that in humans, these 'thin stripe' layers of V2 are selective for colour, and that they project to anatomically distinct columns in V3, which are also selective for colour (Nasr et al., 2016). 'Thick stripes' in V2 and V3 are selective for disparity processing. Therefore, the monocular colour pathways in V1 could also be propagated through V2 and V3. However, areas of ocular dominance have not been consistently found outside of V1, suggesting that despite the separation of colour and disparity information in V2 and V3, neurons supporting colour processing may still be binocular (Nasr et al., 2016).

In terms of colour cells, V4 shows a similar pattern of organisation to earlier visual areas. Central V4 has direct projections from V1 in macaques (Nakamura et al., 1993), and may therefore inherit some of its neural architecture. Like in V1, colour-selective neurons in V4 cluster together, sometimes dubbed 'globs' in reference to the 'blobs' of V1. These 'glob' cells are narrowly tuned for hue, and less sensitive to

luminance or orientation than ‘inter-glob’ cells (Roe et al., 2012). Like V2, V4 is separated into functional ‘stripes’ which selectively respond to colour or orientation (Tanigawa et al., 2010a). However, also like V2, there is no evidence of ocular dominance columns representing the right and left eyes in V4. The disparity tuning of many V4 cells further adds to the interpretation that cells in V4 are binocular (Watanabe et al., 2002). In VO1 and VO2, there has been no investigation of ocular dominance or binocularity of neurons, however, there is a general assumption that these areas are fully binocular, being later visual areas.

Overall, it seems likely that considerable binocular integration of chromatic signals does occur in V1, but that there are parallel processing pathways that extend to V2, V3, and possibly V4, which inherit information from neurons at the centre of ocular dominance columns, and therefore may integrate information from each eye at a later stage. Later visual areas VO1 and VO2 are suggested to be solely binocular, and to only contain pre-integrated representations of colour between both eyes.

1.7.1 Binocular interactions in colour adaptation

Although adaptation likely occurs at multiple stages of the visual system, it remains unclear which specific loci are responsible for the perceptual changes observed in long-term colour adaptation. One method for inferring the site of adaptation is to examine whether the effects transfer between the eyes. If adaptation is occurring at a cortical locus (which would receive binocular input), effects of adaptation would be expected to transfer between the eyes, whereas if it is happening at an earlier stage, before binocular integration, this interocular transfer would not be expected. Interocular transfer of visual aftereffects is generally attributed to the role of binocular neurons in the cortex, and the transfer of the aftereffect is usually smaller than the same-eye aftereffect, which is thought to be due to the involvement of monocular neurons in the creation of the aftereffect. Interocular transfer has been observed for a variety of visual aftereffects, including motion, size, orientation, and spatial frequency (Blake et al., 1981), suggesting a cortical locus for many types of visual adaptation.

Interocular transfer of long-term adaptation can be tested by adapting one eye to a chromatically altered environment, such that unique hues are altered in that eye, then testing if unique hues are also altered in the unadapted eye. Some studies have found no evidence of interocular transfer of chromatic adaptation effects, suggesting that colour adaptation effects remain eye-specific after short term adaptation (Lovegrove et al., 1979), long term adaptation (Eisner & Enoch, 1982, Delahunt et al., 2004), or even for colour-contingent aftereffects such as the McCollough effect (McCollough, 1965). In contrast, other studies have found evidence of interocular transfer of hue shifts after adaptation to colour contrast (Krauskopf et al., 1982), long term adaptation (Neitz et al., 2002), and the McCollough effect (Kaufman et al., 1981a). However, there are still very few studies that have considered whether long term chromatic adaptation effects transfer interocularly, and the studies that do exist often rely on small sample sizes. For example, the evidence for interocular transfer from Neitz et al.'s study is based on a single participant, highlighting the need for more robust investigations.

It is also possible that colour information in the cortex could be processed predominantly by monocular neurons, which might explain the absence of interocular transfer even if long-term adaptation occurs cortically. There is some indirect evidence that suggests that colour neurons may be monocular, such as findings of poor stereopsis for isoluminant (purely chromatic) stimuli (de Weert, 1979; Kingdom & Simmons, 1996), and the cytoarchitectural observation that colour-sensitive neurons are found in 'blobs' in the centre of ocular dominance columns (Horton & Hubel, 1981; Landisman & Ts'O, 2002; Livingstone & Hubel, 1984). However, direct recordings have suggested that there are populations of colour-selective neurons in the macaque cortex that are driven by stimulation from both eyes (Peirce et al., 2008), and that there are strong binocular interactions evident in SSVEPs for both structured and unstructured chromatic stimuli (Carter et al., 2025). It therefore seems likely that colour perception in the cortex involves binocular mechanisms, and therefore we would predict interocular transfer of hue shifts following long term adaptation.

Information from each cone type may also be combined in 'non-canonical' pathways that bypass the primary visual cortex. Different cone types may therefore have

differences in binocular combination, as they may be combined at different stages of the visual system. For example, there may be a direct S-cone pathway from the LGN to MT that bypasses V1 (Sincich et al., 2004a). This means that presenting colours monocularly vs binocularly may have a different effect on hue perception depending on which colours are used. For example, when comparing monocular and binocular hue perception, Opper & Volbrecht (2017) found that there were differences in monocular and binocular hue perception for red and green, but not for blue or yellow. This could imply that binocular integration may affect red/green perception more than blue/yellow perception. Consequently, the nature of chromatic adaptation could differ depending on whether it occurs monocularly or binocularly, and these effects may further vary depending on the specific colours involved in the adaptation process.

1.8 Conclusions

The evidence reviewed here demonstrates that adaptation to a chromatically altered environment leads to systematic shifts in hue perception in the direction of the adapting colour. While retinal adaptation mechanisms can explain some of the shifts in hue perception after adaptation, these are insufficient to explain long-term changes in our perception of colour, which can persist for days, weeks, or months after adaptation. The evidence suggests that chromatic adaptation occurs on multiple timescales and likely involves mechanisms at multiple stages of the visual system. Short-term adaptation appears to be governed by fast, low-level processes with rapid recovery rates, while medium- and long-term adaptation may require higher-level, cortical involvement. The theory of long-term renormalisation in adaptation is supported by some evidence but may not be a complete explanation of how long-term adaptation occurs, as it does not account for non-linearities in adaptation. Moreover, the literature highlights several factors that may modulate adaptation but remain poorly understood, for example, differences in the adaptability of individual cone pathways.

Overall, chromatic adaptation appears to occur on multiple timescales and at multiple levels of the visual system. The physiological mechanisms underpinning

long-term chromatic adaptation are still not well characterised, and the locus of this adaptation is still a matter of debate. The extent to which adaptation requires active input to de-adapt, and the transfer of adaptation between the eyes, may be avenues to explore in order to investigate these questions. Developing a more comprehensive model of adaptation requires integration of findings across a range of timescales and environmental contexts.

Chapter 2: Methods

“The conventional methods of physics are completely adequate to specify a physical stimulus that generates a sensation of colour, but the relationship between the physical stimulus and the magnitude of the sensory response is the concern of the science of psychophysics.”
(Robertson, 1978)

Much of the work in this thesis was completed using a psychophysical approach on an original Wright colorimeter. A multiprimary system allowing silent substitution in conjunction with fMRI was also used in one study. As both of these methods are unusual for different reasons (the colorimeter due to its antiquity, and the multiprimary system due to its recency!), this chapter will expand on the equipment and techniques used to record the data presented in this thesis.

2.1. The Wright Colorimeter

In 1928, WD Wright published a detailed description of a new piece of equipment he had constructed, based on a spectrometer, in order to allow for colour matches to be made between a single wavelength of light, and a mixture of three primaries (Wright, 1928). This machine - the tristimulus colorimeter - would be used by Wright and Guild to determine the colour matching functions, which later led to the development of the CIE colour space. Incredibly, nearly a century later, the 1934 model of the Wright colorimeter used by Wright and Guild in their pioneering experiments is still fully operational, and able to be used in colorimetry research to this day.

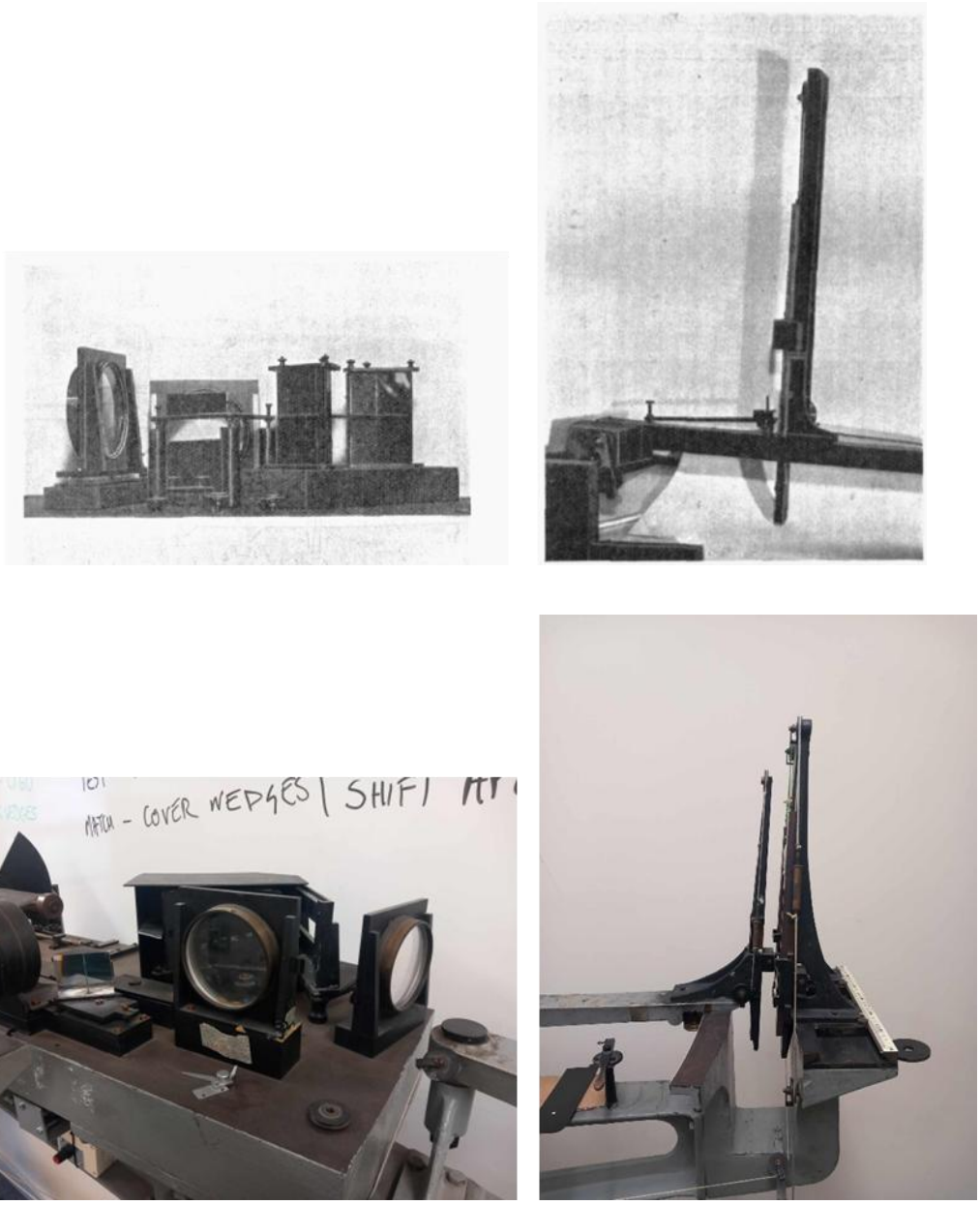
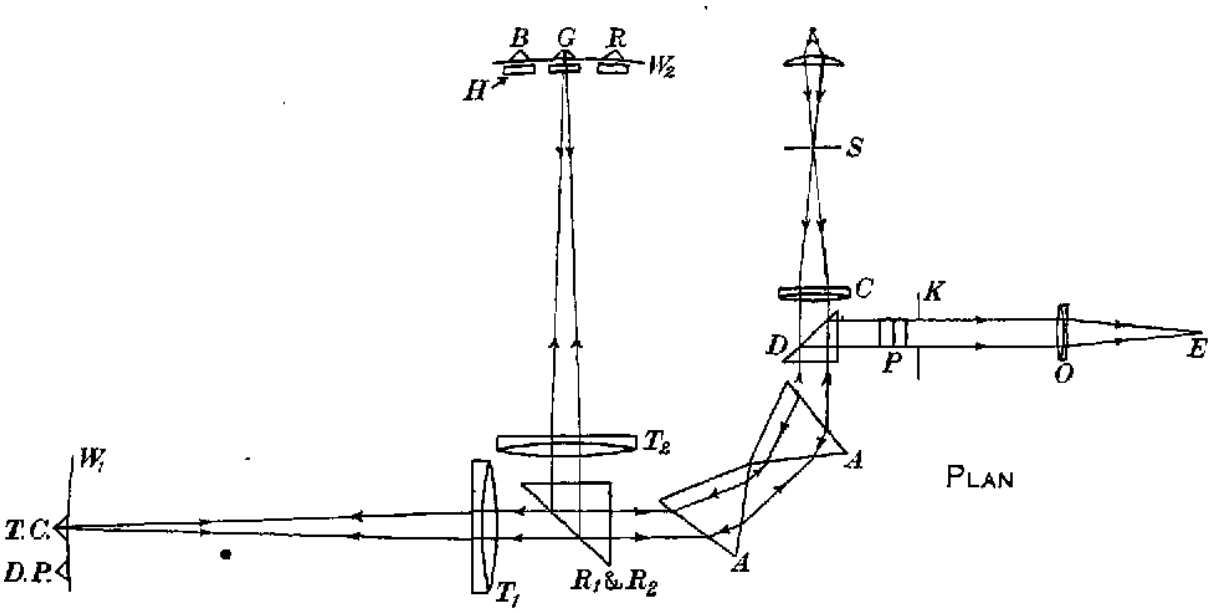


Figure 2.1: *Photographs published by Wright in his 1928 paper, compared to photos taken of the later 1934 colorimeter in the present day. The photos show the refracting and concentrating prisms in the centre of the colorimeter, and one of the arms which reflects the spectrum back towards the observer.*

The colorimeter works by presenting two colours to an observer through a narrow aperture. One colour is constructed by a prism, which splits white light into a monochromatic spectrum about 25cm long. A precise wavelength can be set by adjusting the portion of this spectrum that is reflected back to the observer using a mirror and another prism to direct the selected portion of the spectrum down a narrow slit and back to the observer. The ‘purity’ of the wavelength that is selected is determined by the size of the roof prism, but it is able to be very precise; as narrow

as 1nm. The second colour is constructed by a similar setup, however, instead of a single point in the spectrum being reflected back to the observer, three points in the spectrum can be selected to act as primaries (usually red, green, and blue). These three points are reflected back to the observer after having been combined by use of a concave mirror to form a single colour. Observers can adjust the intensity of each of the primaries in order to produce a colour match to the reference colour produced by the monochromatic spectrum.



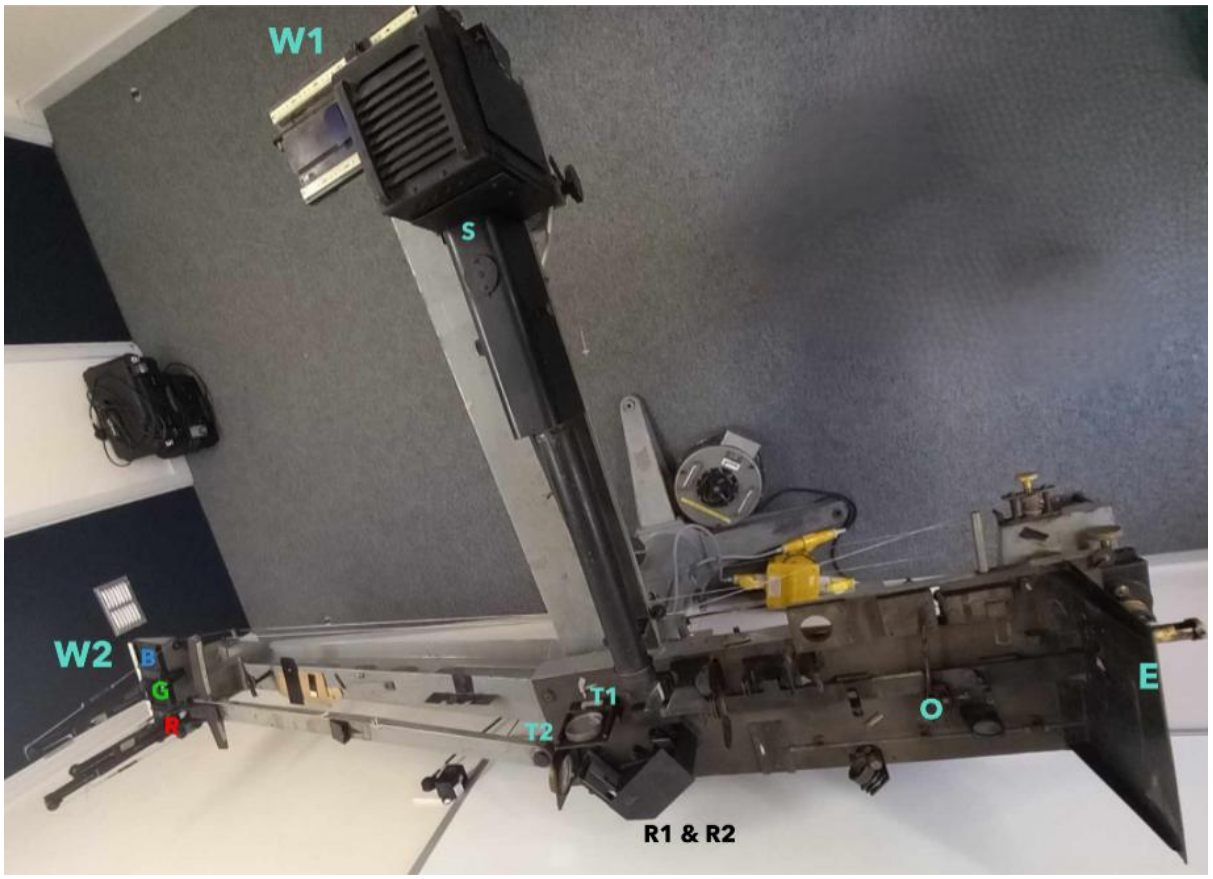


Figure 2.2: *Wright's 1928 diagram of a colorimeter as seen from above. The two arms that produce the reference colour and the tristimulus colour can be seen in the top diagram, which is an aerial view of the apparatus, with W1 being the beam of the reference colour, and W2 being the beam of the tristimulus colour. The arrowed lines depict the path that a beam of light would take through the system. E denotes where the eye of the observer would be. S denotes the collimator slit, which is the first point at which the light is directed into the system, i.e. the origin of the beam. b: A photograph of*

the 1934 colorimeter in the present day as seen from above. This version is slightly developed from the diagram above (e.g. W1 and W2 are reversed) but operates on the same principles. Letters have been added to allow cross-reference of the parts of the colorimeter between the diagram and photograph, where this is known.

2.1.1 Historical Use of the Colorimeter

The original purpose of the colorimeter was to be used in colour matching experiments. Wright (1928-9) and Guild (1925) were the first to perform these experiments, which involved asking observers to colour match a test field with a series of reference colours by adjusting the intensity of each of the primaries to alter the matching stimulus. In order to account for negative matches (in which the reference stimulus cannot be matched because a true match would require a negative value of one of the three primaries), the reference stimulus and primaries had filters applied, in order to facilitate all matches (as without filters, negative values of one primary were sometimes needed to achieve a match). From these experiments on 17 colour-normal observers, Wright and Guild were able to derive colour matching functions, which varied surprisingly little between the participants. Colour matching functions describe how much of each primary is needed in order to match a reference colour. The resulting RGB values (referred to as tristimulus values) can be converted into chromaticity coordinates by removing the element of luminosity, and only keeping the information on the proportions of each primary used to create the colour. This requires the calculations:

$$r = R/(R+G+B)$$
$$g = G/(R+G+B)$$
$$b = B/(R+G+B)$$

The rgb values can be plotted against each other for every potential value at every chromaticity. Because these values are proportions, the total always adds up to 1; therefore, the third value can be inferred from the first two, allowing the values to be plotted in two dimensions. Wright's discovery of this in 1931 led to the creation of the CIE colour space, which continues to be used to numerically specify the proportions

of three primaries which are needed to accurately reproduce a given colour. Interestingly, the first requested use of the CIE colour diagram was from the Ministry of Agriculture, which wanted to define the colour of forced rhubarb numerically.

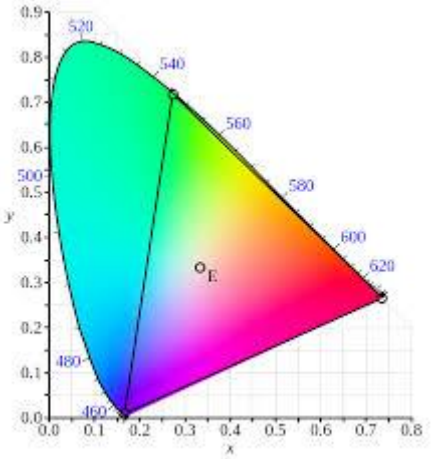


Figure 2.3: *CIE Colour Space. The points on the outer edge are the chromaticity coordinates of spectral colours. Taking any three points on this outer edge gives a triangle which describes the colours that can be created through the mixture of those three primaries.*

2.1.2 Use of the Colorimeter in the Present Research

In the studies presented in this thesis, a key outcome measure was unique hues. Unique hues are the colours red, green, yellow, and blue, which stand out as being described only as themselves, rather than as a combination of other colours (for example, orange may be described as a mixture of red and yellow, but yellow is not described as a mixture of red and green). Unique yellow is described as the point at which an observer judges a shade of yellow to be neither red nor green, while unique green is described as the point at which an observer judges a shade of green to be neither blue nor yellow. Although there is variation across the population in these judgements, an individual in the same state of adaptation will tend to be very consistent in these judgements, particularly for unique yellow. Although it is debated as to whether there is any physiological correlate of unique hues, they provide a useful measure of subjective colour experience that is easily understood by participants.

Unique hues can be set on a colorimeter very simply by only using the reference stimulus, and shutting off the tristimulus colour input. Observers use the method of adjustment in order to set the hue that conforms to the description of unique yellow

or unique green in a 0.67° x 1.33° field. Settings are made in a dark room to prevent there being other colour reference points available to participants, and after five minutes of dark adaptation, in order to ensure photopigments were regenerated to allow for consistent measurements. In Chapter 3, a 4Hz square wave flicker was applied to reduce short-term adaptation to the stimulus (to mitigate the risk of the test stimulus as a source of adaptation), however, it was found that there was not a significant difference in settings made with or without the flicker, and participants reported finding it more difficult to make the settings with the flicker in place, so this was removed in Chapters 4 and 5.

Participants also set Rayleigh Matches in Chapters 3-4, in order to monitor bias and consistency in participants, to check for colour normalcy, and to ensure adaptation did not break down Rayleigh Matches (which would affect unique hue judgements). A Rayleigh Match describes the ratio of red to green light that must be set to allow a colour match to a monochromatic yellow wavelength. Although the colour appearance of the stimulus may change after adaptation, the ratio of red to green needed to match it should not change, according to the law of persistence of colour matches (von Kries, 1904). For example, a participant may make the pre-adaptation Rayleigh match using a 60:40 red-green ratio. After adaptation to red, this colour will appear greener, as the visual system will be discounting a larger part of the red in the colour mixture. However, as the patch to be matched will also appear greener due to the adaptation, the 60:40 red-green ratio will still match the test patch, despite its altered appearance. A colorimeter is designed to make such matches. The blue channel of the tristimulus arm was shut off to give the tristimulus colour as a mixture of red (671nm) and green (557nm), while the reference arm was set to 575nm with a 0.6 neutral density filter in order to reduce the luminance to facilitate colour matches. Observers viewed the two stimuli through a 1.33°x1.33° bipartite field, and were able to adjust the intensity of the red and the green light in order to match the reference stimulus in hue and brightness. Rayleigh Matches were averaged across ten measurements and converted to log(R/G) using the relative radiance of the red and green primaries. As no significant differences were found in any condition, Rayleigh matches were not performed in Chapter 5.

2.1.3 Calibration

In order to be able to report the wavelengths set on the colorimeter, it was necessary to calibrate the centimetre scale on the colorimeter to the equivalent wavelengths. The colorimeter was calibrated using a fibre-optic photospectrometer (*Jaz Spectrometer (Model 44-543)*., n.d.) operating at 2 nm resolution with a 30° integrating lens. Multiple measurements were taken at steps of 1cm and averaged. A fourth order polynomial function was then used to fit the data and generate a lookup table for scale readings at 0.05 cm resolution. A simple script was used to convert the scale readings for each participant to the equivalent wavelength before averaging.

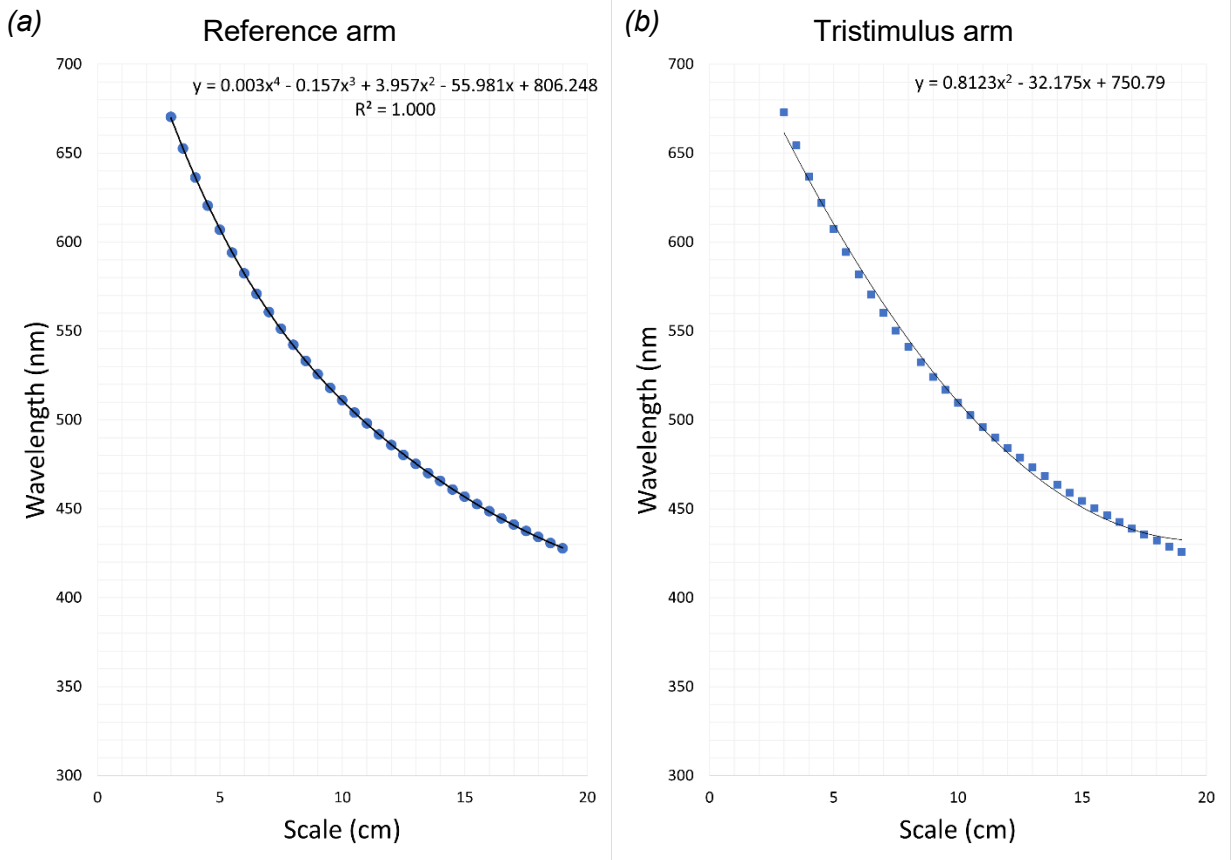


Figure 2.4: *(a) Colorimeter scale plotted against recorded wavelength for the reference arm. (b) Colorimeter scale plotted against recorded wavelength for the tristimulus arm*

2.2. Filter Measurements

In order to adapt participants in the experiments described in Chapters 3-5, it was necessary to acquire some kind of chromatic filter. Previous experiments had used a mixture of coloured goggles, coloured contact lenses, and filtered lighting (e.g. Eisner and Enoch, 1982, Neitz, 2002, Belmore and Shevell, 2011). We chose to use colour-filtered goggles, as this allowed participants to move around flexibly while also being relatively easy to set up. Lee colour filters (Lee filters 106 Primary Red and 713 Winter Blue, Lee Filters, Andover, UK) were affixed to clear goggles in order to create the adapting environment (shown in Figure 2.5). The transmittance of the filters at each wavelength was measured using a photospectrometer (Jaz Spectrometer (Model 44-543)) operating at 2 nm resolution with a 30° integrating lens.

Figure 2.5: *Goggles used to adapt participants. In the top photo are full-field goggles used in Chapters 3 and 4. In the bottom photo are the eye-isolating goggles used in Chapter 5.*

In order to measure the transmittance of the filters, the spectrometer was used to measure the spectral irradiance of a reference National Institute of Standards and Technology (NIST)-traceable light source. The filters were then applied to this reference light source and the reference measurement divided by the filter measurement in order to give the relative transmittances (Figure 2.6). This was performed using the PySilSub toolbox (J. Martin et al., 2023)

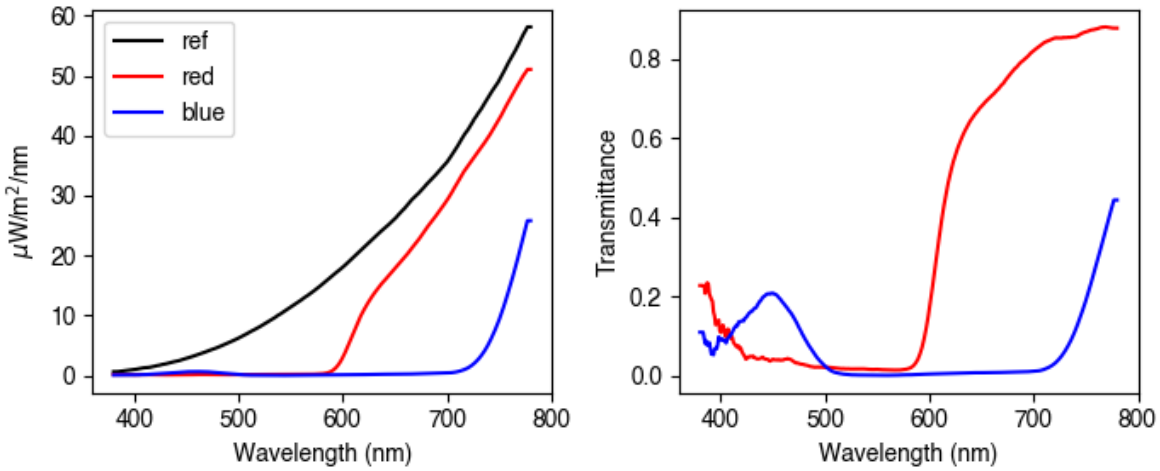


Figure 2.6: *(a) The spectral irradiance of the reference light source, and with the red and blue filters applied. (b) The calculated transmittance of the red and blue filters. Measurements taken with a Jaz spectrometer (Ocean Optics).*

We then multiplied these transmittance spectra with Stockman's 2-degree fundamentals (Stockman & Sharpe, 2000) in order to estimate the amount that each cone would be stimulated by a white light source filtered through either the red or the blue goggles. As can be seen in the graph below, the red filter mostly suppresses S-cones and M-cones. While there is residual activity in both S-cones and M-cones, the M-cones are suppressed to a much greater extent than L-cones, so we can predict that the L/M cone ratio will be altered. The blue filter suppresses L-cones and M-cones at long wavelengths, although there is still some residual sensitivity at lower wavelengths which may lead to a slight change in L/M ratio as well as a change in S/(L+M) ratio.

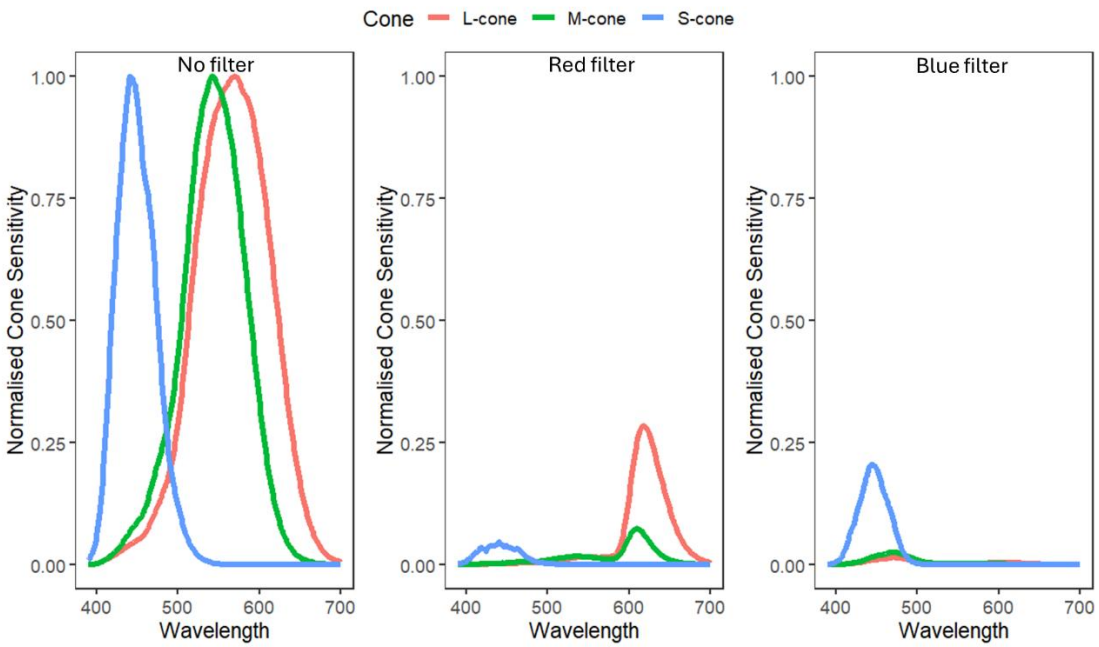


Figure 2.7: *Normalised cone sensitivities under normal illumination, under the red filter condition, and under the blue filter condition.*

In Chapter 3, neutral density filters with different levels of luminance transmission were applied to the red filter (Lee filters 209 0.3ND, 210 0.6ND, and 211 0.9ND, Lee Filters, Andover). Here, luminance refers to the photometric measure of the light intensity transmitted, expressed in candela per square metre (cd/m²). The luminance transmissions of the neutral density filters combined with the red filter were recorded using a Minolta photometer (Konica Minolta, Tokyo, Japan) and a background white light with a luminance of 85.83 cd/m^2. The recorded measurements were converted into log units and plotted, showing a linear decrease in luminance spanning about 10 log units. The luminance transmittance of the blue filter used in Chapter 3 was also measured and compared to the red filters. The results are shown in Figure 2.8.

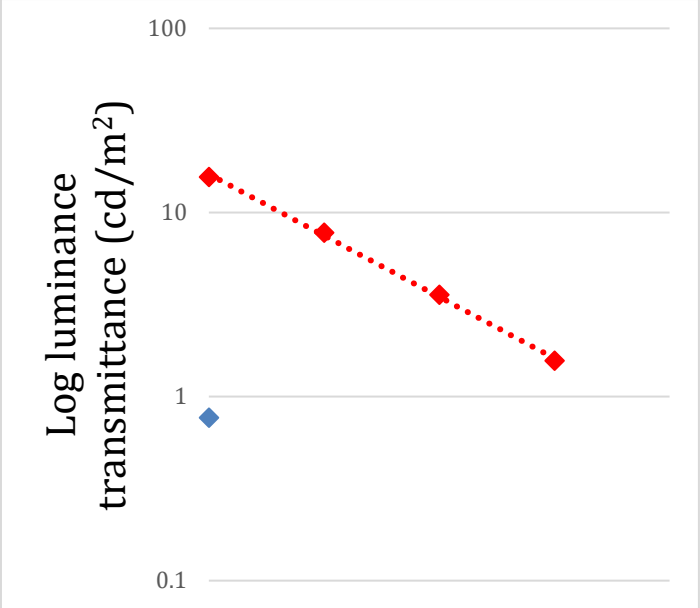


Figure 2.8: *Comparison of red filter luminance transmissions with each neutral density filter, and blue filter luminance transmission (measured in cd/m2). Each point represents a different filter luminance transmission. The red points represent the four red filters; the blue point represents the blue filter.*

2.3. Multiprimary System and Silent Substitution

In Chapter 6, the goal was to be able to isolate different receptor classes in each eye individually while recording monocular and binocular fMRI responses from the visual cortex. Due to the overlap in cone sensitivities, it is a challenge to find stimuli that can stimulate just one cone class without also producing interfering stimulation in the other classes of photoreceptor. One technique that aims to resolve this issue is silent substitution (see Spitschan & Woelders, 2018 for full review). Silent substitution involves alternating two wavelengths to selectively stimulate only one class of photoreceptor while keeping the activation of all other classes constant. For example, let us say that in M cones both a wavelength of 515nm and a wavelength of 575nm cause a response of 0.8 a.u. In L cones, the wavelength of 515nm will cause a response of 0.6 a.u. but the wavelength of 575nm will cause a response of 1 a.u. This means that (in the absence of other photoreceptor types) any observed change occurring in the visual system when those two wavelengths are presented can be attributed to the change in the response of L cones, rather than due to M cones, as there is no change in the M cone response. An example of a theoretical probe that would silence M cones but not L cones is illustrated in Figure 2.9.

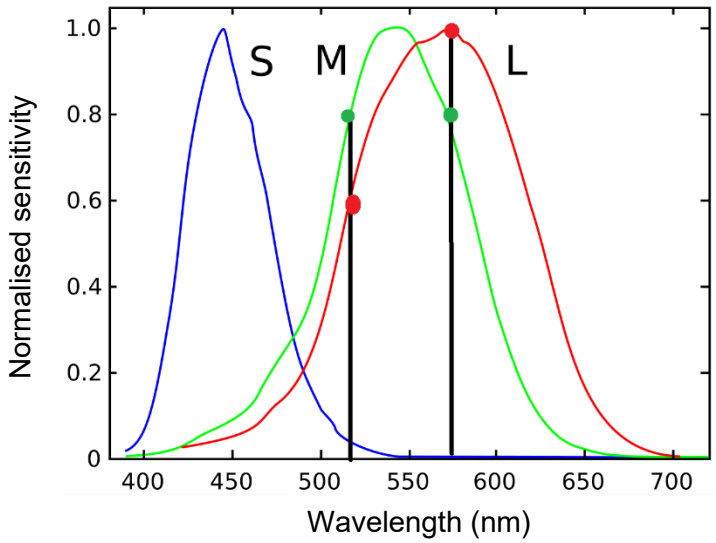


Figure 2.9: *A hypothetical condition in which M cones are silenced by selecting two wavelengths that produce the same magnitude of response in M cones but not in L cones.*

It is relatively easy to find wavelengths that silence one photoreceptor type. However, the challenge comes in finding wavelengths that, for a certain luminance, are able to appear metameric to every class of photoreceptor except one, especially when an experiment intends to control for the potential interference of rods and melanopsin. In the above example, while the M cones would be silenced, rods and melanopsin would also have different magnitudes of response in the 515nm condition compared to the 575nm condition. One solution to this is to use very high light levels, such that rods would be completely saturated all the time, however, computer screens have a limited luminance, and increasing luminance would not silence melanopsin, which this study wanted to control for. It is possible to achieve silent substitution of all photoreceptor classes but one (N-1) by having the same number of primaries as photoreceptors (N). This is relatively simple if only the cone classes are targeted, as N = 3, but when rods and melanopsin are taken into account, N = 5, and so at least five primaries are needed to achieve silent substitution. The spectral sensitivities of all five classes of photoreceptor are shown in Figure 2.10.

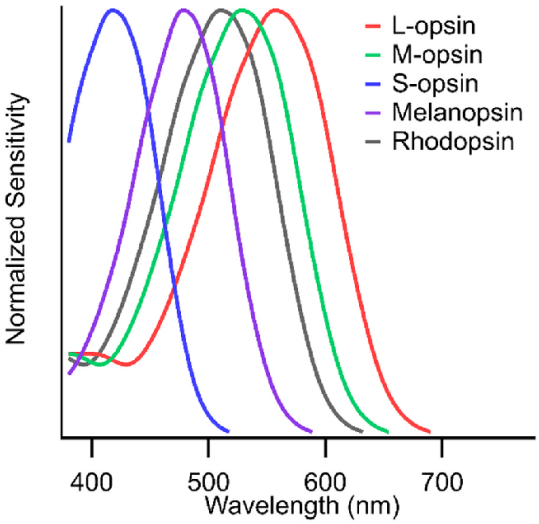


Figure 2.10: *The sensitivity functions of all five classes of photoreceptor pigment in the human eye. From (Patterson et al., 2021)*

One frequent approach to calculating silent substitution solutions is to use linear algebra to calculate the intensities of each primary needed to produce certain changes in activation in each receptor type, and isolate solutions where the intensity changes activation in one receptor type only. The system of primaries on the device and photoreceptors in the eye can be entered into a matrix equation.

$$E = S * I$$

where:

E = vector of receptor excitations (size = n photoreceptors)

S = "sensitivity matrix" (size = n photoreceptors * n primaries), describing how much each receptor type responds to each primary

I = vector of light intensities for each primary (size n primaries)

We need two wavelengths to alternate, so we need two values of I (I_1 and I_2). These will create two different values of E (E_1 and E_2) according to the equation above. The aim is to find values of I_1 and I_2 where the change in E ($E_1 – E_2$) gives a non-zero value (and ideally a value as far away from zero as possible) for one receptor class, while equalling zero for all other receptor classes. This problem can be described as:

$$\Delta E = \Delta I * S$$

As S is a known series of values, these can be input to the matrix. Linear algebra can then be used to solve for the values of I that fulfil the criteria of causing a change in E for one receptor class but maintaining a change of zero in the others.

To achieve silent substitution, we used two 10-primary LEDMOTIVE STlab devices (SpectraTuneLAB: LEDMOTIVE Technologies, LLC, Barcelona, Spain) which could stimulate each eye independently. These light devices were calibrated using a Jaz photospectrometer (Ocean Optics) and Stockman and Sharpe's (2000) 10 degree cone fundamentals. The devices were attached via liquid light guides (LLG3-8H: Thorlabs Ltd, Cambridgeshire, UK) to two eyepieces of diffusive and semi-opaque white glass discs, which were mounted on a modified VR headset (SHINECON SC-G01, Dongguan Shinecon Industrial Co.). The viewing distance was adjusted for each participant in order to ensure they were able to fuse the stimulus between the eyes, compensating for individual differences in focal length. The light guides were attached to the light engine diffusers with threaded adapters (SM1A9, AD3LLG: Thorlabs Ltd, Cambridgeshire, UK), and the exiting ends were attached to optical cylinders (SM2L20: Thorlabs Ltd, Cambridgeshire, UK) via threaded adapters (AD3LLG, SM2A6: Thorlabs Ltd, Cambridgeshire, UK). In order to guarantee safe illumination levels, a neutral density filter of 0.6 log units was placed between the light source and the diffuser discs. The set-up is shown in Figure 2.11.

The light devices were operated using a Python interface (J. Martin et al., 2022) which allowed simultaneous sequences of stimuli to be presented in each eye. The stimuli seen were two flickering discs spanning 30 degrees of visual angle. The central 7 degrees of visual angle were obscured in both eyes using a small piece of blackout material, in order to prevent differences in macular pigment density or alterations in the cone mosaic in the fovea from interfering with silent substitution calculations. Silent substitution values were calculated using the PySilSub toolbox using linear algebra for each participant, considering lens yellowing as a function of age using the CIE 2006 Physiological Observer (J. Martin et al., 2023).

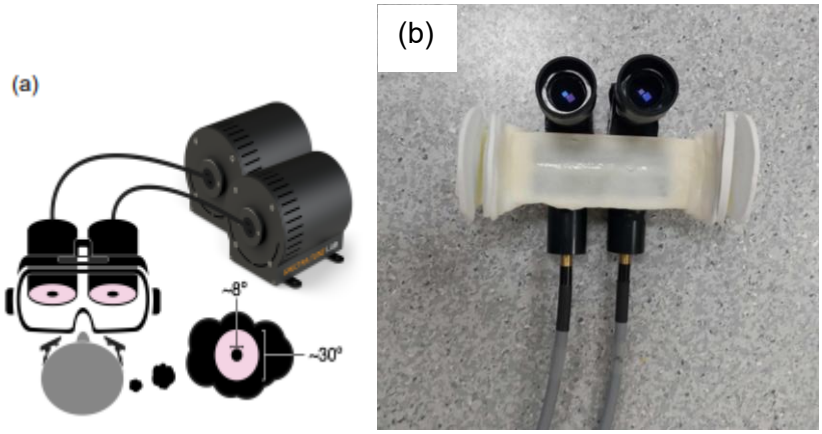


Figure 2.11: *(a) A schematic of the multiprimary STLAB system. The participant views a disc stimulus independently with each eye, which is fused into a single percept by the observer. From (Segala, 2023) (b) The fMRI-suitable setup of the modified VR headset, through which participants viewed the stimuli.*

Chapter 3: Effects of Duration and Light Intensity on Chromatic Adaptation Aftereffects

Long-term chromatic adaptation may involve global renormalisation of cone signals, resulting in an enduring shift of unique hues by around 5nm (Neitz *et al.* 2002). We sought to determine the effect of adaptation duration, adapting colour, and light intensity on the shift in unique yellow measured five minutes after adapting to coloured goggles. We investigated what length of time was sufficient to induce a shift in unique yellow settings, whether adaptation strength was dependent on the colour of adaptation, and the effect of different levels of light intensity on adaptation. Participants made unique yellow and unique green wavelength settings after adaptation to red or blue filtered light. Settings were made using the method of adjustment of a small rectangle on a Wright colorimeter. Results suggested that shifts in unique yellow appearance increased between 15 minutes and 60 minutes of adaptation, but were not significantly different between 60 and 240 minutes. This pattern suggests that this form of adaptation is distinct from short-term (photoreceptor) adaptation, as significant shifts in unique hue perception persisted five-minutes post-adaptation, and continued to increase after the point of photoreceptor adaptation saturation. The light intensity of the adapting environment had a linear impact on the size of the shift in unique hue, with larger shifts occurring after adaptation to higher light intensities, implying a 'dose-dependent' effect of the adapting environment on chromatic adaptation.

3.1 Introduction

When the colour of our environment changes, our vision adapts to maintain the most accurate colour perception of the world around us, maintaining or restoring the world to a "normal" colour appearance. This adaptation can occur at a number of different time scales. Previous research has suggested that adaptation involves two mechanisms: a rapid, short-term mechanism that maintains consistency across a scene, and a long-term mechanism that changes the baseline of our expectations and lasts for hours or days (K. E. Tregillus & Engel, 2019).

Short-term adaptation to colour occurs on a time scale from a few milliseconds to a few minutes, with the majority (50-60%) of adaptation occurring virtually instantaneously, and the remaining adaptation occurring over a time course of seconds to minutes (A. Werner et al., 2000). While short term adaptation may occur at various stages of the visual system, it is traditionally explained by Von Kries adaptation in the photoreceptors. Von Kries adaptation involves adjusting cone responsiveness based on the illumination of the environment. In environments where the global illumination disproportionately stimulates one or more cone types, the responsiveness of that cone class can be decreased (von Kries, 1905). This type of adaptation saturates quickly, and recovers quickly.

However, some types of chromatic adaptation are more enduring, and may last for multiple days. The duration of these perceptual changes is far longer than the endurance of rapid photoreceptor adaptation that is thought to underlie short term adaptation. In one experiment, Eisner and Enoch (1982) adapted participants monocularly with a red filter worn continuously for a week, observing progressively larger shifts in unique yellow over time, which persisted for hours or even days after adaptation to the filter ended. In another demonstration of long-term adaptation, Neitz *et al.* (2002) adapted participants to red- or green-filtered environments for 4-12 hours per day, over 8-25 days. The shift in unique yellow settings increased steadily throughout the adaptation period, regardless of its duration, and persisted for several days after exposure ended. Neitz *et al.* suggest that this effect can be explained by a cortical renormalisation mechanism that uses visual experience to adjust L/M gain control. This normalisation mechanism calibrates the red/green opponent system to be in ‘equilibrium’ for the average illuminant of the environment, as sampled over an extended duration. The effects of this normalisation mechanism can be measured through subjective perception of yellow, as this is often considered to be determined by the ‘null’ or ‘zero’ point of the L/M channel. If L and M cones are contributing equally to the perception of yellow (i.e. a gain control factor of 1.00), Neitz *et al.* calculate that unique yellow should be, on average, around 545nm. However, true measurements of unique yellow place it on average around 578nm. L cones would need to be dampened by a factor of around 0.64 in order to shift the L/M ratio to a point where the zero point of the mechanism lands at 578nm (Figure

3.1). This suggests that gain control factors can be stored over long periods of time, in order to determine our perception of colour.

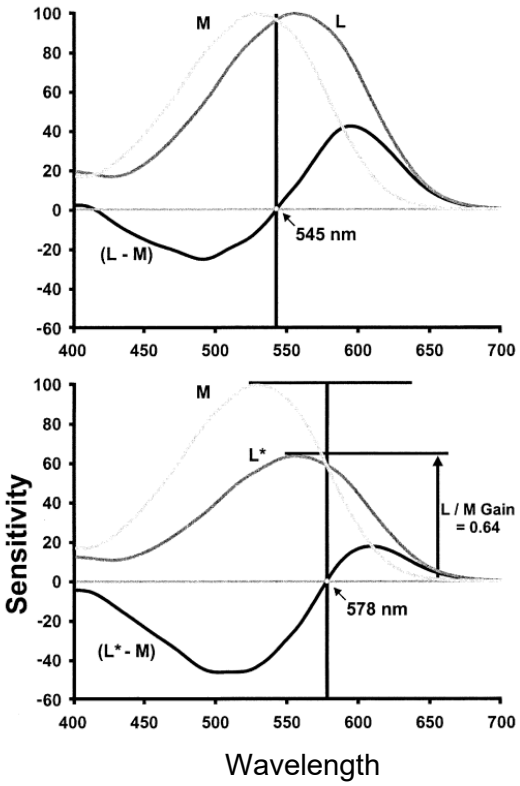


Figure 3.1*: Demonstration of the gain factor needed to produce a 'zero' point in the L-M mechanism that coincides with 578nm. From Neitz et al., 2002.*

However, it is likely that there is also a process of chromatic adaptation that exists between the rapidity of photoreceptor adaptation, and the longevity of cortical renormalisation. Shimakura & Sakata (2022) suggest that there is a post-receptoral process of chromatic adaptation that may saturate within 20-60 minutes of adaptation to an altered colour environment. Li et al. (2020) similarly suggest that this type of chromatic adaptation builds up over a period of around one hour. The characterising factor of this adaptation that separates it from long-term adaptation is the speed of its recovery; instead of persisting for hours or days, the adaptation effects decay quickly. This timescale of adaptation remains relatively unexplored, and varies considerably between individuals (Li et al., 2020). It remains unclear how long an adaptive environment must be sustained to fully saturate medium-term adaptation mechanisms, or how long it must persist to begin engaging more enduring long-term adaptation processes.

Furthermore, long-term adaptation has only been studied in terms of readjustment of red/green colour contrast channels. Research suggests that yellow-blue cancellation functions are consistent across the retina, despite large differences in the filtration of light through the macular pigment, and would therefore imply that the yellow/blue colour contrast channels can also be adapted (Hammond, 2008). However, it is unclear whether S-cone-dependent channels would adapt in the same way as L/M-cone-dependent channels. S-cones have a lower sensitivity than L and M cones, and so may have a higher threshold for adaptation. This may mean that longer durations of an adaptive environment may be needed to saturate S-cone pathways compared to L/M adaptation.

In the present study, Experiment 3.1 aims to investigate whether long-term adaptation mechanisms can be engaged within 15 minutes, 60 minutes, or 240 minutes of exposure to an altered chromatic environment, as measured by the change in unique yellow settings after adaptation, and the rate at which unique yellow settings return to baseline after recovery. Long periods of adaptation would lead to extended saturation of short-term adaptive mechanisms, and therefore we might expect longer-term adaptive mechanisms to begin to be engaged, if the two mechanisms are linked. This experiment also aims to investigate whether adapting to different chromatic environments affects the strength or pattern of adaptation, by adapting participants to either red or blue environments.

We predicted that longer durations of adaptation would lead to larger shifts in unique hues, and that these shifts would be in opposite directions for adaptation to red versus blue (with shifts towards longer wavelengths after adaptation to red and shorter wavelengths after adaptation to blue). For the blue adaptation condition, we also measured participants' unique green settings, as there was a possibility that blue adaptation would not lead to large changes in unique yellow compared to unique green. The same predictions applied as for the unique yellow condition.

We also anticipated that shifts in unique hues may be detectable 60-minutes post recovery after 240 minutes of adaptation, but not after shorter durations. We also tested participants' Rayleigh matches before and after adaptation as a control (in order to ensure that these did not break down after adaptation, as this could imply

optical changes or methodological issues) and predicted that these would not change.

We also performed some exploratory analyses on points of interest in the data. We investigated whether there was any significant decay in adaptation aftereffects during the course of the testing session, which lasted 5-10 minutes, as if the adaptation were to be due to rapid cone adaptation that had not completely decayed over 5 minutes, then we would expect to see a significant trend in unique hue settings towards pre-adaptation settings during the testing session. Furthermore, we noticed large variability between the size of the shift in unique hue settings following adaptation between different participants, and investigated whether this was systematic.

During data collection for Experiment 3.1, it was observed that there was a large difference in brightness (i.e., the subjective lightness) between the red and the blue goggles, with the red goggles being much brighter than the blue. A result of this may be that the overall light levels of the adapting environment may also have a role in the adaptive state of the visual system. Wright (1946) adapted participants to coloured lights of different intensities across 180 seconds, and showed that lower intensities of adapting light decrease the magnitude of the reduction in red and green sensitivity post-adaptation, and that red and green sensitivity recovers faster when the adaptation stimulus had a lower light intensity. Adaptation, therefore, may be 'dose-dependent', building up across time spent in a colour altered environment, but also dependent on the light intensity of that environment. Previous studies into medium (Li et al., 2020) and long-term adaptation (Neitz et al., 2002), and Experiment 3.1 presented here, have not accounted for differences in the light intensity of the adapting environment, with participants normally given free choice of activity while adapting. If light intensity has an impact on the size of the adaptive shift experienced, then it may explain some of the individual differences found in previous research. When interpreting the results of Experiment 3.1, it is important to consider that differences in the magnitude or pattern of adaptation between the red and blue conditions may be due to differences in the photometric luminance of the filters, rather than differences in the spectral composition of the light.

In Experiment 3.2, participants were adapted to red goggles with neutral density filters applied, which altered the intensity of the adapting environment in each condition. Four different levels of neutral density filter were tested, and unique yellow measurements were recorded, with the aim to investigate the impact of changing the intensity of the adapting environment on the shift in colour perception. We predicted that goggles with higher luminance transmissions would cause larger shifts in unique yellow following adaptation.

3.2 Experiment 3.1: Time course of adaptation at different durations and chromaticity of environments

3.2.1 Methods

Participants

Six participants (3 male, 3 female, 4 naive, 2 non-naive) participated in both the red and the blue adaptation conditions. An additional five participants (1 male, 4 female, 4 naive, 1 non-naive) participated in the red adaptation condition only, and an additional five participants (3 male, 2 female, 5 naive) participated in the blue adaptation condition only, for a total of 11 participants in each condition.

Participants were aged between 18-60 and were colour-normal observers as assessed by Rayleigh matching. Informed consent was obtained in accordance with the ethical permission granted by the University of York Department of Psychology Ethics Committee.

Design

A mixed model design was used in which the between-subjects factor was filter colour (red or blue) and the within-subjects factors were measurement time (pre-adaptation, post-adaptation, and post-recovery), and adaptation duration (15 minutes, 60 minutes, or 240 minutes). Outcome measures were unique hues (unique yellow in all conditions, unique yellow and unique green after adaptation to blue).

Apparatus

Participants were adapted using red or blue filtered goggles, which filtered out the majority of wavelengths below 600 or above 500 respectively. More details on the properties of the goggles can be found in Chapter 2 (2.2. Filter Measurements).

Unique Hues measurement

Monochromatic light (subtending .67° x 1.33° visual angle) was presented via a tristimulus colorimeter (Wright, 1928, 1934) and altered using the method of adjustment. For unique yellow (UY) measurements, participants were instructed to turn a dial that shifted the stimulus wavelength along a monochromatic spectrum, and to stop when the stimulus appeared neither red nor green (uniquely yellow). In the blue condition, participants were also asked to make unique green (UG) judgments, setting the stimulus to be neither yellow nor blue. Starting points along the monochromatic spectrum were randomly selected, and it was alternated whether the starting point tended towards longer or shorter wavelengths on the spectrum relative to the range of unique hue settings. Participants made 11 UY judgments in each session and their average UY was calculated from the last 10 UY settings. The same method was applied to Unique Green measurements in the blue condition. A 4Hz square wave flicker was applied to prevent short term adaptation to the light source. Measurements were taken in a dark room.

Rayleigh Match

Rayleigh matches were presented via a tristimulus colorimeter, and subtended 1.33° x 1.33° visual angle. The upper half of a stimulus corresponded to a monochromatic light set to 575nm. This reference wavelength was determined by measuring the unique yellow settings of two pilot participants and taking their average unique yellow setting. The lower half of the stimulus corresponded to a mixture of red (671nm) and green light (557nm). Participants were asked to use two dials to alter the luminance of the red and green light sources in order to match the upper half of the stimulus in terms of both hue and brightness. Six Rayleigh matches were averaged and converted to log(R/G) using the relative radiance of the red (R) and green (G) primaries.

Procedure

Participants remained in the colour-altered environment for 15 minutes, 60 minutes, or 240 minutes in each condition. Each period of adaptation took place on different, non-consecutive days to prevent any multi-day build-up of adaptation effects. Testing occurred before wearing the goggles (pre-adaptation), 5 minutes after removing the goggles (5-post-adaptation), and 60 minutes after removing the goggles (60-post-adaptation). Before each testing session, participants were dark-adapted for five minutes. Each testing session consisted of 11 unique hue settings, then 6 Rayleigh Matches, in the right eye only, and took around 10 minutes to complete.

While wearing the goggles, participants were told to continue their day normally, experiencing their normal range of environments. Participants reported that they mostly remained indoors, looking at computer screens. After removing the goggles and completing the testing session, participants then spent 45 minutes in normal illumination conditions as a recovery period.

Statistical Analysis

Results were analysed using three-way mixed model ANOVAs with follow-up analyses using one-way ANOVAs and post-hoc t-tests. These analyses were performed in R, and the ANOVAs were performed using the afex package. Bayes Factor analyses were also run, in order to be able to verify the presence or absence of reliable effects. These were performed using JASP.

In the ANOVA and Bayes Factor analyses, participants' UY values were averaged across all trials within a condition, in order to give the most representative value of unique yellow. However, an alternative approach is to use linear mixed effect modelling to capture the variance in unique hue across a testing session, as this incorporates all trials in a testing session, by setting the subject as a random effect. Linear mixed effect models were run using the lme4 and lmerTest packages in R.

3.2.2 Results and Discussion

Changes in Post-Adaptation Shifts in Unique Yellow

The wavelength settings for unique yellow are plotted for the three testing times (pre-, 5-minute post and 60-minute post adaptation) for the different adaptation durations

(15, 60 and 240 minutes) and colour of adaptation (red or blue) in Figure 3.2. These plots demonstrate two features: (1) that there are shifts in UY setting for the 5-minute post adaptation test condition compared to pre-adaptation, and (2) that the shifts are in opposite directions after adaptation to red and blue, shifting towards redder and greener shades respectively. The 5-minute post-adaptation UY settings also differed in some conditions depending on the duration of adaptation.

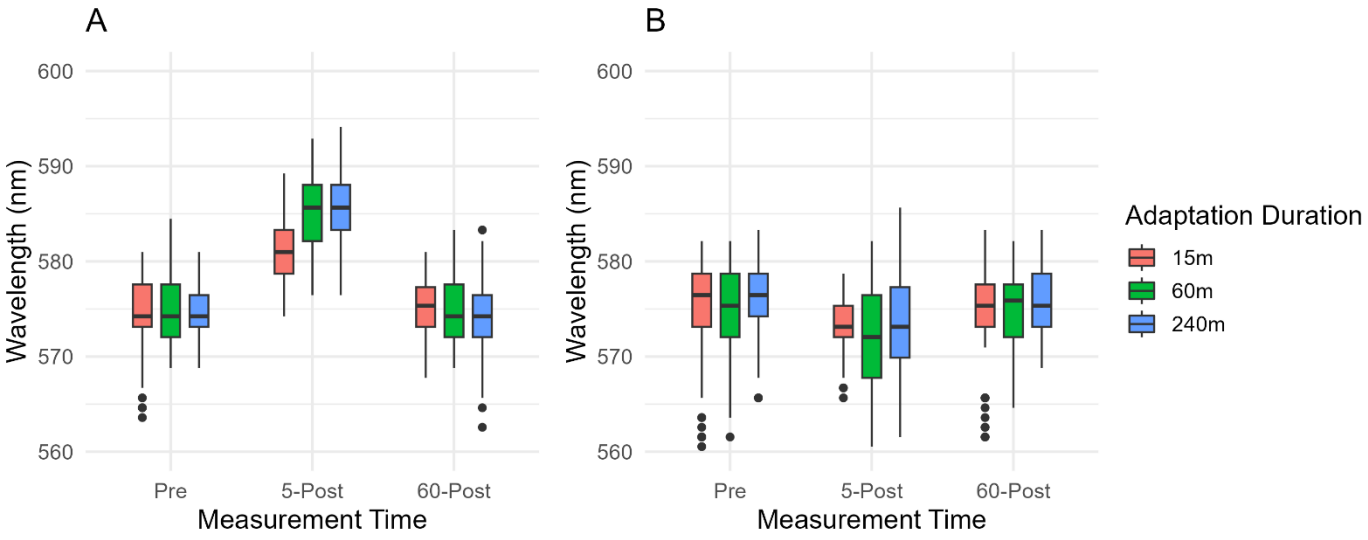


Figure 3.2: *A: Unique Yellow settings in the red condition for each level of adaptation duration measured pre-adaptation, post-adaptation, and post recovery, B: Unique Yellow settings in the blue condition for each level of adaptation duration measured pre-adaptation, post-adaptation, and post recovery.*

We compared UY across all conditions in both the red and the blue filter experiments. The UY settings differed between the red and blue conditions, and between the measurement points of pre-adaptation, 5-minutes post-adaptation, and 60-minutes-post adaptation. In order to establish the significance of the pattern of results, we ran a three-way mixed model ANOVA. This indicated a significant three-way interaction between adaptation colour, UY measurement time, and adaptation duration ($F(4, 80) = 4.41$, $p = .003$, $\eta^2_p = .181$), which permitted us to run further follow up analyses.

To follow up we first performed two-way ANOVA on the colour adaptation conditions (red and blue) separately, allowing us to investigate the main effects of adaptation duration and the time at which UY settings were made with respect to the adaptation,

and their interaction. It is noted that the three-way interaction in the previous analysis could largely have been driven by the red and blue adaptation conditions having similar effects of the other independent variables, but with opposite signs, reinforcing the need to approach the analysis of the conditions separately.

The two-way repeated measures ANOVA of the UY settings for the red adaptation condition showed an interaction between measurement time and adaptation duration ($F(4, 40) = 10.47$, $p = <0.001$, $\eta^2_p = .511$), suggesting that UY settings changed between measurement timepoints to different extents after different durations of adaptation. In addition, there was a main effect of measurement time ($F(2, 20) = 123.55$, $p = <.001$, $\eta^2_p = .925$), which Figure 3.2 would suggest is driven principally by differences in UY settings at the 5-post adaptation timepoint. However, there was no main effect of adaptation duration ($F(2,20) = 1.94$, $p = .169$), which may be because of similar settings at the pre-adaptation and 60-post-adaptation timepoints across adaptation durations. Bonferroni-corrected post-hoc t-tests indicate that the significant main effect of measurement time was driven by significant differences between pre-adaptation and 5-minute post adaptation ($t(32) = 13.83$, $p <0.001$), and 5-minute and 60-minute post adaptation ($t(32) = -13.72$, $p <0.001$), but not between pre-adaptation and 60-minute post adaptation ($t(32) = -0.75$, $p = 1.000$), as predicted visually from Figure 3.2. Given the absence of differences between the pre and 60-minute post adaptation, we reasoned that the interaction was driven by adaptation duration dependent effects at the 5-minute post-adaptation timepoint.

In the blue adaptation condition, we ran a two-way repeated measures ANOVA with the same variables as for the red adaptation condition. This time, there was no significant interaction between adaptation duration and measurement time in the two-way repeated measures ANOVA ($F(4, 40) = 0.33$, $p = .854$), which suggested that, unlike in the red adaptation condition, UY settings did not change between measurement timepoints as a function of adaptation duration. Like the red adaptation condition, there was not a significant main effect of adaptation duration ($F(2,20) =1.22$, $p = .316$), but there was a main effect of measurement time ($2, 20) = 24.53$, $p = <.001$, $\eta^2_p = 0.710$). We analysed this main effect with post-hoc Bonferroni-corrected t-tests, and found that the effect was driven by significant differences between pre-adaptation and post adaptation ($t(32) = -7.48$, $p = <0.001$), and post

adaptation and post-recovery (t(32) = 5.85, *p* = <0.001), but not between pre-adaptation and post-recovery (t(32) = -1.6, *p* = 0.359). The results for the blue adaptation are consistent therefore with those from red adaptation in terms of measurement time. However, unlike the red adaptation condition, the results suggest that while there was a shift in UY settings post-adaptation, this shift did not significantly change in magnitude across adaptation durations.

In order to incorporate within-subject variation, linear mixed-effects models were run on the entire dataset, including all trials from all participants. Participants were input as random effects, and measurement time (pre, 5-post, 60-post) and adaptation duration as fixed effects. Measurement time was dummy-coded with pre-adaptation as the reference level. Adaptation duration was also dummy-coded as a factor with 15 minutes as the reference level; treating this as categorical provided a more stable model fit than treating this as numeric.

For the red adaptation condition, the model showed a significant increase in UY settings from pre to 5-post adaptation (t(11.75) = 7.55, p < .001), but no significant difference between pre and 60-post adaptation (t(17.07) = 0.50, p = .623). Neither the 60-min nor the 240-min adaptation duration differed significantly from the 15-minute duration at the pre-adaptation time point (t(11.25) = 0.61, p = .552; t(11.37) = −0.04, p = .967). However, both the 60 and 240 minute adaptation durations showed significant interactions at the 5-post measurement time (60-minute: t(924.05) = 9.10, p < .001; 240-minute: t(925.98) = 11.92, p < .001), indicating that the changes in UY settings from pre to 5-post were substantially larger for both the 60-minute and 240-minute adaptation durations compared with the 15-minute duration. The 60-minute adaptation duration did not show a significant interaction with the 60-post measurement time (t(924.05) = −1.85, p = .064), indicating no reliable differences from the 15-min duration. However, unexpectedly, the 240-minute duration did show a significant interaction with the 60-post measurement time (t(924.05) = −2.08, p = .038), suggesting settings were significantly different at the 60-post measurement point in the 240-minute adaptation condition compared to the 15-minute adaptation condition. This pattern of results generally corroborated the significant results found in the ANOVA, with the exception of the significant difference in 60-post UY settings in the 240-minute adaptation duration condition compared to the 15-minute

adaptation duration condition. This was especially unexpected as the UY settings in the 15-minute condition at the 60-post timepoint were further from the pre-adaptation baseline than in the 240-minute condition. This was contrary to the prediction that longer periods of adaptation would have slower recoveries.

For the blue adaptation condition, the model also showed a significant change in UY settings from pre- to 5-post adaptation (t(13.93) = -6.29, $p < .001$), but no significant difference between pre- and 60-post adaptation (t(24.65) = -1.27, $p = .215$). Neither the 60-minute nor the 240-minute adaptation duration differed significantly from the 15-minute duration at the pre-adaptation time point (t(10.91) = 0.60, p = .954; t(10.86) = 1.10, p = .295). The 60-minute adaptation duration did not show significant interactions with the 5-post measurement time (t(930.99) = 0.21, p = .834), indicating that the changes in UY settings from pre to 5-post were not significantly different between the 15- and 60-minute adaptation conditions. However, unlike in the ANOVA, there was a significant interaction between the 15-minute and 240-minute adaptation durations and the 5-post measurement time (t(930.99) = 2.36, $p = .018$), suggesting that the change in UY settings at the 5-post measurement point differed significantly between the 15- and 240-minute conditions. Neither the 60 or 240-minute adaptation duration showed a significant interaction with the 60-post measurement time (60-minute: t(930.99) = 0.74, p = .459; 240-minute: t(930.99) = −4.55, p = .649), indicating no significant differences from the 15-minute duration. This pattern of results differed to the ANOVA, in that it highlighted a smaller change in UY post-adaptation in the 240-minute adaptation condition.

In Figure 3.3, in the red adaptation condition, we can observe apparent differences in UY shifts in unique yellow settings between the 15-minute and 60-minute conditions, but not between the 60-minute and 240-minute conditions. In order to provide evidence for this pattern of results, we ran Bayes Factor paired t-tests on the pre to 5-post unique yellow shift between the 15-minute and 60-minute 5-post conditions, and the 60-minute and 240-minute 5-post conditions, hypothesising that unique yellow shifts should be larger in longer adaptation duration conditions. After adaptation to the red filter, this test indicated strong evidence for a larger unique yellow shifts in the 60-minute condition compared to the 15-minute condition (BF_{10} = 52.61), but no evidence for larger unique yellow shifts in the 240-minute condition

compared to the 60-minute condition (BF_{10} = 1.00), which supported the visual interpretation of the data.

For the blue adaptation condition, Figure 3.3 suggests that there was no difference in UY shifts between different adaptation durations. In order to provide evidence for this, we ran Bayes Factor paired t-tests with the hypothesis that unique yellow shifts should be larger at longer adaptation durations. This test indicated no evidence for larger unique yellow shifts in the 60-minute condition compared to the 15-minute condition (BF_{10} = 0.28), and no evidence for larger unique yellow shifts in the 240-minute condition compared to the 60-minute condition (BF_{10} = 0.33), which supported the visual interpretation of the data.

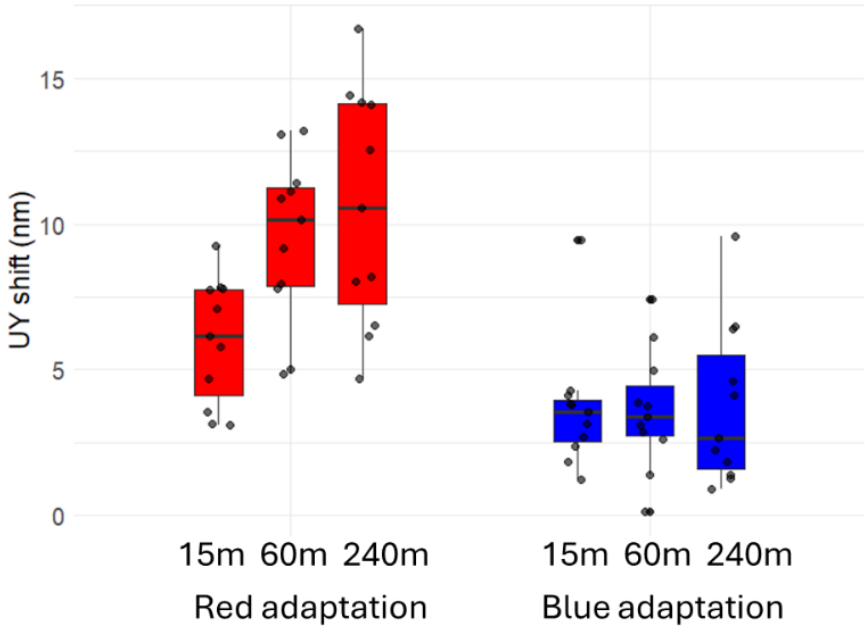


Figure 3.3: *Shift in unique yellow between pre- and 5-post adaptation for red and blue for each duration condition after adaptation to red or blue filters. Each point represents a single participant.*

Rayleigh matches

Participants' Rayleigh Matches were analysed using a three-way mixed-model ANOVA. This indicated no significant interactions between adaptation colour, adaptation duration, and measurement time. In addition, there were no significant main effects of adaptation colour (p = .901), or adaptation duration (p = .561), or measurement time (p = .063). Figure 3.4 plots the Rayleigh Match data across filter colour, adaptation duration, and measurement time. These findings are in line with

established research suggesting that Rayleigh Matches are consistent across a large range of adaptation and chromatic conditions, and implies that the adaptation occurring in this study does not cause non-linearities in colour perception that would break down Rayleigh Matches.

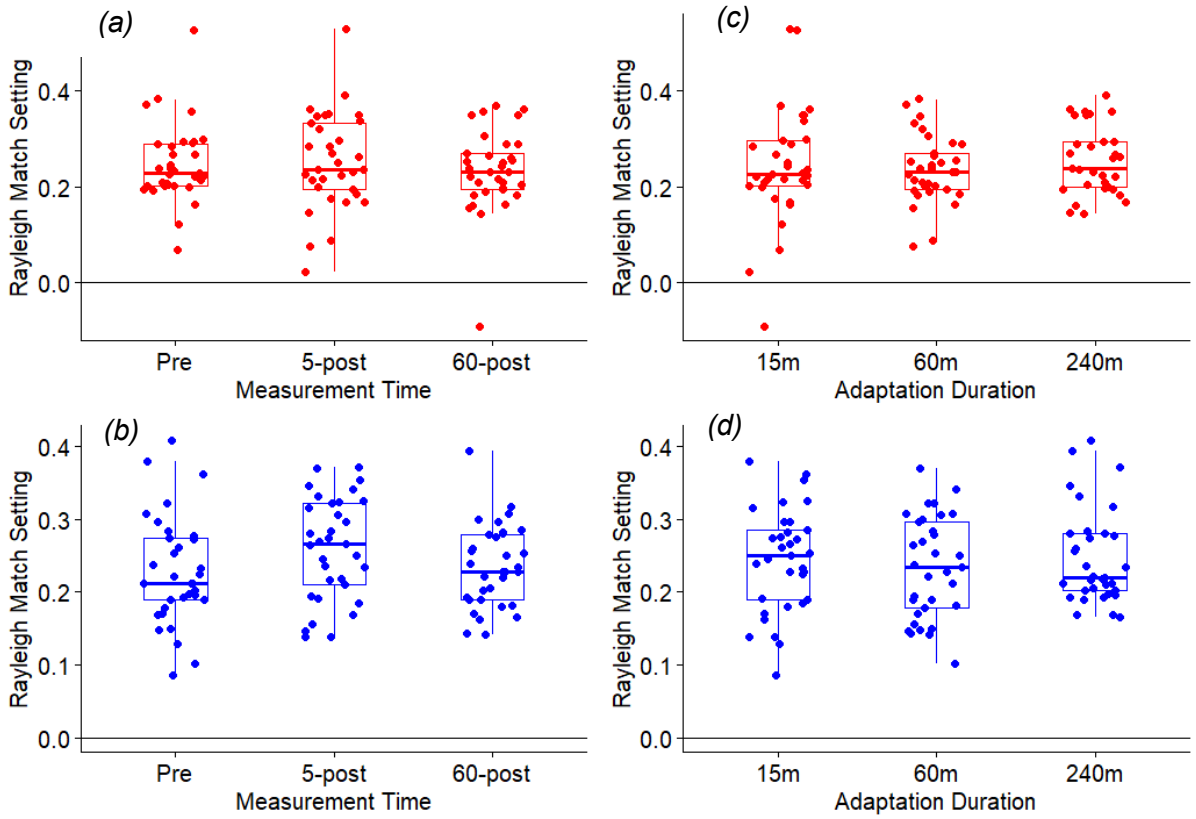


Figure 3.4: *Graph showing Rayleigh matches for the red and blue conditions. Rayleigh Matches do not change as a function of adaptation duration or measurement time. A) Rayleigh Match settings across adaptation durations for each measurement timepoint after adaptation to the red filter. B) Rayleigh Match settings across adaptation durations for each measurement timepoint after adaptation to the blue filter. C) Rayleigh Match settings across measurement timepoints for each adaptation duration after adaptation to the red filter. D) Rayleigh Match settings across measurement timepoints for each adaptation duration after adaptation to the blue filter. Each point represents a single testing session.*

Changes in Post-Adaptation Shifts in Unique Green

We noted that in the blue adaptation condition, one potential reason for the smaller effect sizes to changes in Unique Yellow could be due to the larger influence of S-cones in the blue condition compared to the red condition, as we would predict that

changes in S-cone sensitivity should impact unique yellow settings less than changes in L or M cone sensitivity. To account for this, we also tested participants' Unique Green (UG) settings in the blue adaptation condition. The results are plotted in Figure 3.5. These data show shifts in Unique Green towards shorter wavelengths after adaptation in all duration conditions, as found when measuring Unique Yellow. There is little difference between the sizes of the shift between the 60-minute and 240-minute conditions, but a slightly smaller shift after 15 minutes of adaptation.

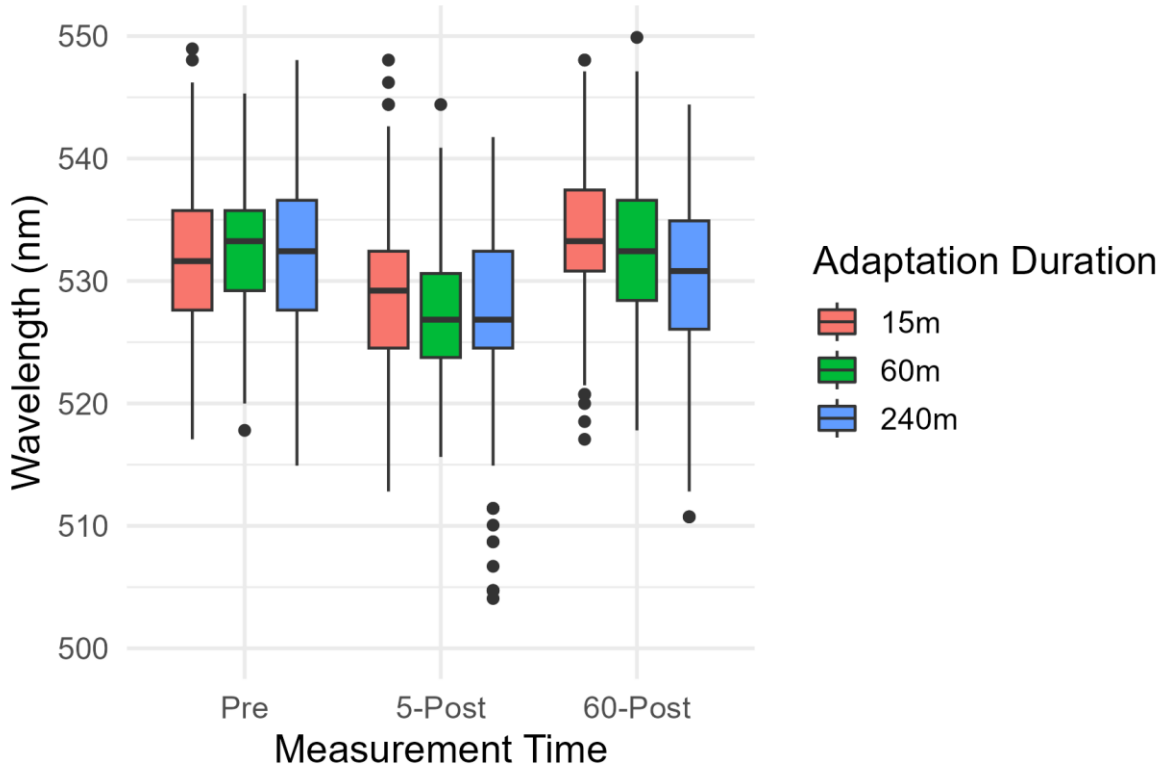


Figure 3.5: *Unique green measurements at pre- 5-minute post, and 60-minute post adaptation measurement timepoints after 15, 60, or 240 minutes adaptation to blue.*

A two-way repeated measures ANOVA was conducted to analyse whether these effects were significant. This showed no significant interaction between adaptation duration and measurement time ($F(4,40) = 1.80$, $p = .190$), nor was there a significant main effect of adaptation duration ($F(2,20) = 0.64$, $p = .511$), although there was a significant main effect of measurement time ($F(2, 20) = 66.60$, $p = <.001$, $\eta^2_p = .869$). This was the same pattern of results as found for unique yellow settings in the blue adaptation condition. This would suggest that there were no differences in the shift in unique green settings between pre- and 5-post after different adaptation

durations. However, in order to test this, and for consistency with the unique yellow analysis, we ran Bayes Factor paired t-tests on the pre- to 5-post unique green shifts between adaptation durations of 15 minutes and 60 minutes, and 60 minutes and 240 minutes, hypothesising that larger adaptation durations would lead to larger shifts. Contrary to the ANOVA, these suggested moderate evidence that there were larger unique green shifts in the 60-minute condition compared to the 15-minute condition (BF_{10} = 6.19), though there was no evidence for larger unique green shifts in the 240-minute condition compared to the 60-minute condition (BF_{10} = 0.19).

The sizes of shift for unique yellow and unique green after adaptation to blue are compared in Figure 3.6. This shows that the sizes of shift were generally larger when unique green was measured (compared to unique yellow) in the 60 minute and 240-minute conditions.

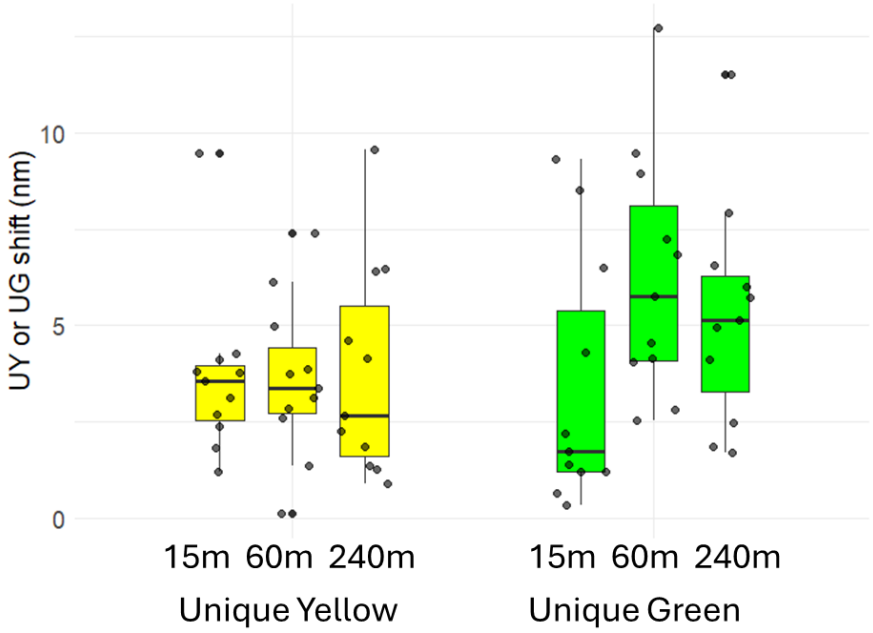


Figure 3.6: *Comparison of the normalised Unique Yellow and Unique Green shifts between the pre-adaptation and 5-minutes post adaptation measurement timepoints, after adaptation to a blue filter. Each point represents a single participant.*

Adaptation Decay Across Trials

While not the primary focus of the experiment, examining the rate of recovery of adaptation aftereffects across the period of testing could be informative. If the adaptation aftereffect were to decay rapidly across the course of the 10 testing trials

(which lasted 5-10 minutes), this may be indicative of a short-term cone effect that had not fully recovered during the 5-minute window of delay. However, the lack of a significant trend towards pre-adaptation settings, or only a small significant effect, across these trials may indicate a longer-term, more enduring effect.

Participants' Unique Yellow settings were compared across trials at each measurement time across all adaptation durations. Linear mixed effect models were used, with participants input as a random effect, and trial and measurement time input as fixed effects, with pre-adaptation dummy-coded as a reference variable for measurement time. In the red condition, the model suggested that there was no significant effect of trial ($t(69.87) = -.73$, $p = .471$), nor were there significant interactions between trial and 5-post adaptation ($t(957.83) = -.88$, $p = .307$), or between trial and 60-post adaptation ($t(957.06) = .12$, $p = .995$). Unique yellow was significantly different from the pre-adaptation timepoint at the 5-post adaptation timepoint ($t(957.03) = 17.97$, $p < .001$), but not the 60-post adaptation timepoint ($t(957.06) = -.65$, $p = .515$). This pattern of results suggests that there is no significant change in UY across trials, regardless of whether this was measured pre-adaptation, 5-post adaptation, or 60-post adaptation, suggesting that there was no significant decay of UY across the post-adaptation testing sessions.

These data, averaged across all participants and all adaptation durations, are shown in Figure 3.7a.

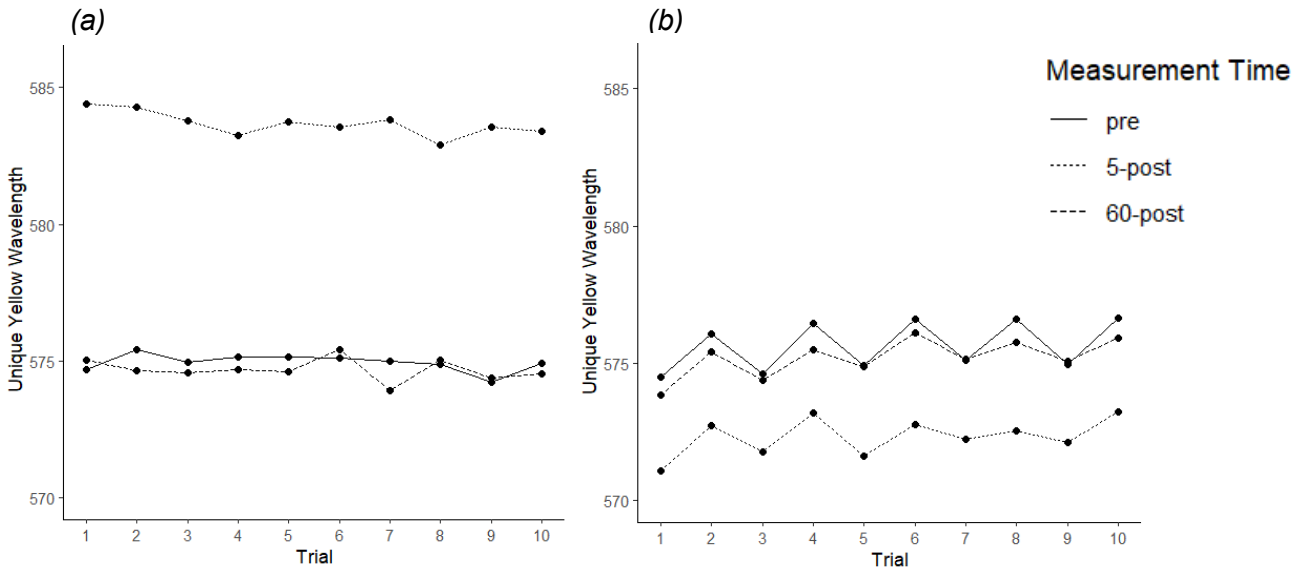


Figure 3.7: *Post-adaptation Unique Yellow settings across every trial in each testing session, averaged across adaptation durations and across participants, in A: the red adaptation condition, B: the blue adaptation condition. Lines represent different measurement timepoints.*

We repeated this analysis for Unique Yellow settings in the blue adaptation condition. Like in the red model, the blue model suggested there was a significant effect of measurement time on UY settings at the 5-post timepoint ($t(974) = -6.61$, $p < .001$), but not the 60-post timepoint ($t(974) = -1.17$, $p = .241$). However, unlike the red model, there was a significant main effect of trial ($t(974) = 2.07$, $p = .039$), although there was no significant interaction between trial and the 5-post timepoint ($t(974) = -.15$, $p = .879$), or between trial and the 60-post timepoint ($t(974) = .31$, $p = .756$). Looking at the data in Figure 3.7b, it seems likely that this main effect is driven by the 'zig zag' effect of participants biasing their unique yellow settings in the direction of the starting wavelength for the method of adjustment. The lack of a significant interaction suggests that unique yellow settings across trials did not change depending on whether unique yellow was measured before or after adaptation.

The lack of a significant interaction suggests that the trend of unique yellow settings across trials did not significantly change depending on whether unique yellow was measured before or after adaptation. However, it is worth recognising that unique yellow settings must be recovering over the course of the testing period (even if this change is sufficiently small as to not be significant over 5 minutes), as unique yellow settings have recovered to pre-adaptation values by 60 minutes post-adaptation. Fitting a linear model to the data suggests that trials in the 5-post red condition have a slope of -.10, and trials in the 5-post blue condition have a slope of .10 (interestingly, showing the same rate of recovery, despite the differences in the absolute size of the adaptation effect). A basic linear extrapolation would suggest that based on this trend, the unique yellow in the red condition would return to pre-adaptation settings in a further 82 trials. As each trial takes roughly 30 seconds, this would suggest that unique yellow settings should return to baseline roughly 40 minutes after the end of the first testing session, if a linear trend continues. For the blue condition, unique yellow should return to pre-adaptation settings within 24 trials, or 12 minutes.

Variance in Adaptation Within Participants

Although the trends in adaptation reported above were consistent across participants, there was considerable variability in the size of unique hue shifts between participants. This is consistent with previous literature which also found individual variation in adaptation. One point of interest was to investigate whether adaptation effects were fairly consistent within the same participant, or whether it varied largely within a participant. The former would suggest that the size of adaptation aftereffects may be determined by internal, intrinsic factors, the latter might suggest that external, changeable factors have a larger influence.

To investigate this, we plotted correlations between the size of the shift in unique yellow between the 15-minute, 60-minute, and 240-minute conditions for red and blue adaptation. The correlations tended to scale with the size of the effect; when effect sizes were larger, correlations were stronger. In the red condition, this resulted in moderate to strong correlations between unique yellow shifts after different adaptation durations. In the blue condition, this resulted in small to moderate correlations. The data and Pearson's correlations are reported in Figure 3.8.

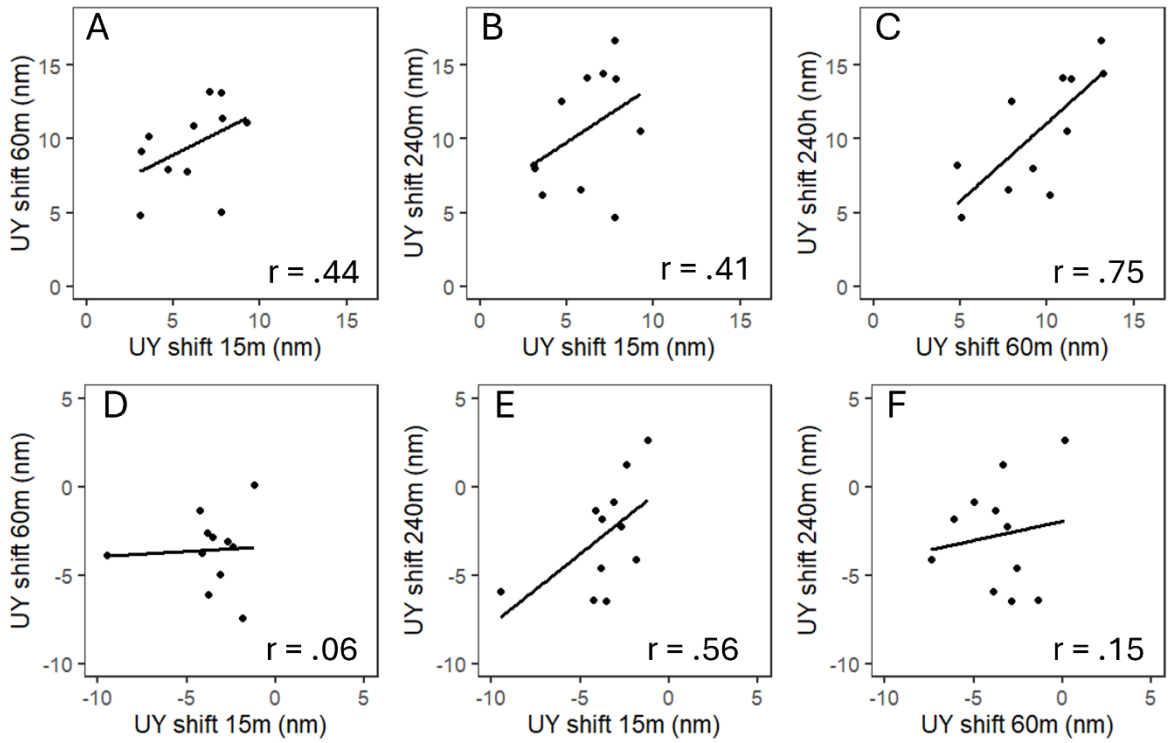


Figure 3.8: *Correlations between the shift in unique yellow settings between the pre- and 5-post-adaptation measurement points at different adaptation durations (Using Pearson's R). Unique yellow has a medium to strong correlation between conditions. A) 15-minute vs 60-minute UY shift after*

adaptation to red. B) 15-minute vs 240-minute UY shift after adaptation to red. C) 60-minute vs 240-minute UY shift after adaptation to red. D) 15-minute vs 60-minute UY shift after adaptation to blue. E) 15-minute vs 240-minute UY shift after adaptation to blue. F) 60-minute vs 240-minute UY shift after adaptation to blue. Each point represents a single participant.

Interim Discussion

The results of this study suggest that 15- to 240-minute adaptation to red or blue environments causes a shift in unique yellow towards longer wavelengths after adaptation to red, and towards shorter wavelengths after adaptation to blue. This shift is present five minutes after adaptation but is not significantly different from pre-adaptation settings by one hour after adaptation. The shift in unique yellow settings increases initially after adaptation to red, likely plateauing at some point between 15 and 60 minutes of adaptation. This is consistent with the results reported by Sakata and Sakamura (2022) that participants' shift in colour settings plateaued between 20 minutes and 1 hour of adaptation. After adaptation to blue, there was less evidence for a significant difference in unique hues after different durations of adaptation, with no significant effects being found between different adaptation durations for unique yellow. However, Bayes factor analyses suggested that there was a difference between the 15-minute and 60-minute conditions when unique green was measured instead. Both unique green and unique yellow shifts were smaller in the blue condition compared to the red condition, suggesting that the magnitude of adaptation aftereffects is reduced after adaptation to blue compared to red.

The shift in unique hues after exposure to a chromatically-altered environment suggests that, as previous studies have found (e.g. Eisner & Enoch, 1882, Neitz *et al.*, 2002, Belmore & Shevell, 2011, Tregillus *et al.*, 2016, Sakata and Sakamura, 2022, Li et al., 2020), it is possible to induce shifts in colour perception through exposure to a biased chromatic environment that persist beyond the timescale of a few seconds. Shifts in unique hues were present when participants were tested five minutes after removing the coloured goggles, suggesting that this type of adaptation cannot be attributed to rapid photoreceptor adaptation. However, our results also suggest that the adaptation we observed was not the same as the long-term renormalisation proposed by Neitz *et al.* (2002). Unlike in long-term adaptation, shifts in colour perception were no different between pre-adaptation and 60-minutes after

adaptation, suggesting that the changes were not enduring. It seems likely that this type of adaptation is occurring on a post-receptoral level, but it is not engaging the cortical renormalisation mechanisms put forward by Neitz et al. This pattern of results also suggests that four hours of adaptation is insufficient to engage long term renormalisation mechanisms; these are likely only engaged after multiple days of exposure to the adapting environment.

The results also demonstrate that shifts in both unique yellow and unique green are present when adapting to blue environments. It is possible that these differences are driven by small differences in the adaptation of the L and M cones; although both L and M cones are largely suppressed, they still retain some sensitivity at short wavelengths, and the M-cones retain slightly more sensitivity than L-cones, reversing the pattern from the red adaptation condition. However, it is also possible that S-cones may be contributing to some degree, as the S/(L+M) ratio will have been changed to a much larger extent than the L/M ratio. The same gain control mechanism that is suggested to exist in L/M pathways (which allows adaptive control of the relative weightings of L vs M cone input) may also account for adaptation of an S-cone dependent pathway.

3.3 Experiment 3.2: Post adaptation UY at different adaptation intensities

As mentioned previously, there was a large perceptible difference in the brightness of the red filter versus the blue filter. Photometric measurements confirmed that the blue filter transmitted substantially less light overall. Although the S-cones would still receive substantial short-wavelength stimulation in the blue filter condition, the overall photon flux reaching the retina was much lower in the blue condition. If the magnitude of adaptive change scales with the number of photons absorbed by the adapting mechanism, then a smaller adaptive shift would be expected under these lower-luminance, blue-filter conditions. This would suggest that the difference in the magnitude of unique hue shifts between the red and blue conditions could arise from differences in effective cone stimulation and photon catch, rather than from fundamental differences in the adaptive properties of the L/M and S/(L+M) pathways.

To investigate this further, Experiment 3.2 compares adaptation to red filters that have the same wavelength transmission, but different luminance transmissions.

3.3.1 Methods

Participants

10 participants took part in this experiment (2 male, 8 female, 5 naïve, 5 non-naïve). All participants took part in all four testing conditions, but for 3 participants who had previously participated in the 1-hour red adaptation condition, their data from this experiment were used for the no neutral density-filter condition, as the experimental protocol was the same. Participants gave their consent for this data to be reused.

Participants were aged between 18-60 and were colour-normal observers as assessed by Rayleigh matching. Informed consent was obtained in accordance with the University of York Department of Psychology Ethics Committee.

Design

We used a within-subjects design in which the within-subjects factor was goggle luminance transmission (of which there were four levels). Outcome measures were unique hues.

Apparatus

Participants were adapted using goggles filtered with Lee acrylic filters, as in the previous experiment (see Chapter 2 for a summary of the spectral transmissions of the goggles and their effects on cone sensitivity (2.2. Filter Measurements).) In addition to the red Lee filter, three of the goggles also had neutral density filters applied, the luminance transmissions of each are in Table 3.1.

Table 3.1: *Luminance transmission of each pair of goggles used in the experiment.*

Filter	Luminance Transmission (cd/m^2)
Red filter (No neutral density filter)	15.596

Red filter + neutral density filter Lee 209	7.764
Red filter + neutral density filter Lee 210	3.578
Red filter + neutral density filter Lee 211	1.566

Unique Hues measurement

Monochromatic light (subtending .67° x 1.33° visual angle) was presented via a tristimulus colorimeter (Wright, 1928, 1931) and altered using the method of adjustment. For unique yellow measurements, participants were instructed to turn a dial that shifted the stimulus wavelength along a monochromatic spectrum. Instructions were given to set Unique Yellow (UY) and Unique Green (UG) by instructing participants to stop the dial when the stimulus appeared neither red nor green, or neither more yellow nor more blue. Starting points along the monochromatic spectrum were randomly selected, and it was alternated whether the starting point tended towards longer or shorter wavelengths on the spectrum relative to the range of unique hue settings. Participants made 11 UY judgments in each session and their average UY was calculated from the last 10 UY settings. The same method was applied to Unique Green measurements. Measurements were taken in a dark room.

Rayleigh Match

The same method of recording Rayleigh matches was used as described in the previous experiment.

Procedure

Participants remained in the red-filtered environment for 60 minutes. Before each testing session, participants were dark-adapted for five minutes. Participants' unique hue and Rayleigh Match settings were tested at three time points: before wearing the goggles (pre-adaptation), 5 minutes after removing the goggles (5-post-adaptation), and either 30 or 60 minutes after removing the goggles (see Chapter 4 for the

rationale for this, and for analysis of the different recovery durations (4.2 Experiment 4.1: Recovery of adaptation effects after adaptation to red filters of different luminance.)).

Statistical Analysis

Results were analysed using two-way mixed repeated measures ANOVAs using the afex package in R, using participants' averaged UY and UG settings. In order to be consistent with previous analyses, linear mixed effect models were run using the lme4 and lmerTest packages in R, using all trials across all conditions. Linear regressions were run in R on participants' average shifts in unique hues between the pre- and 5-post adaptation timepoints, using the base R lm function, in order to quantify the effect of light intensity on the magnitude of the change in unique hue.

3.3.2 Results and Discussion

The pre- and post-adaptation wavelength settings for unique yellow (UY) and unique green (UG) for each level of filter luminance transmission are plotted in Figure 3.9. The data suggest that the size of the adaptation aftereffect decreases with decreasing light intensity of the adaptive environment.

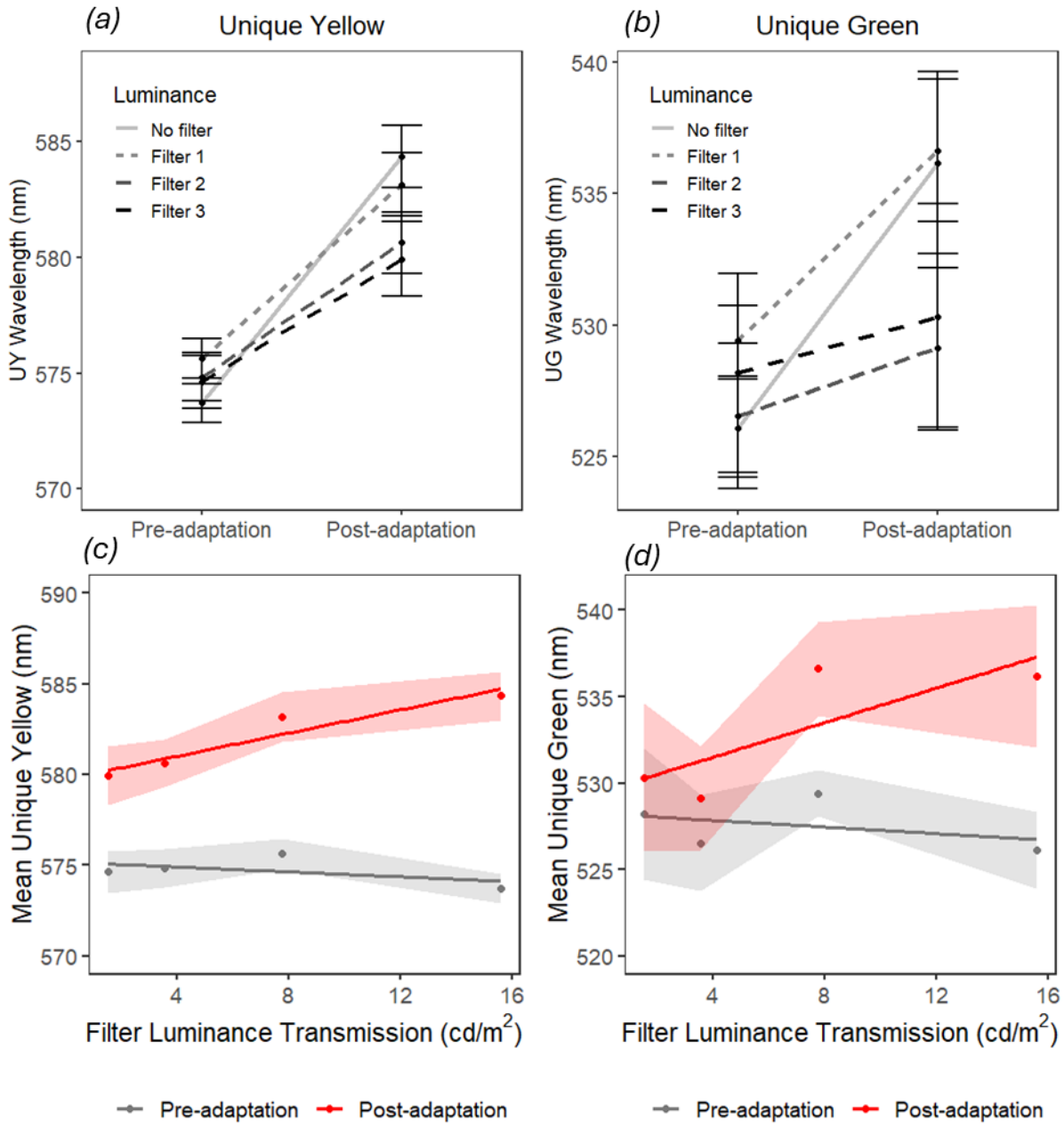


Figure 3.9: *A: Mean Unique Yellow settings at each measurement point for each filter used. B: Mean Unique Green settings at each measurement point for each filter used. Error bars represent +/- one standard error of the mean. C: Mean shift in Unique Yellow between pre- and 5-post-adaptation for each luminance condition. D: Mean shift in Unique Green between pre- and 5-post-adaptation for each luminance condition. Lines represent a linear model y~x fitted to the data. The shaded regions represent +/- one standard error of the mean.*

Two-way repeated measures ANOVAs were performed for both UY and UG in order to investigate the relationship between light intensity and unique hue settings. The factors included were light intensity (no filter, filter 1, filter 2, filter 3), and measurement timepoint (pre- or post-adaptation), and the outcome measures were

either unique yellow or unique green. The UY ANOVA showed a significant interaction between measurement time and light intensity ($F(3,27) = 12.87$, $p < .001$), and a significant main effect of measurement time ($F(1,9) = 148.25$, $p < .001$), though not a main effect of light intensity ([GG] $F(1.67,15.06) = 2.92$, $p = 0.092$). The ANOVA performed on the UG data showed the same pattern, with a significant interaction between measurement time and light intensity ($F(3,18) = 5.59$, $p = .004$), and a significant main effect of measurement time ($F(1,6) = 20.99$, $p = .007$), but no main effect of light intensity ($F(3,18) = 1.52$, $p = .245$).

In order to be consistent with the previous experiment, a linear mixed effect model was also conducted on the data. These were run separately for UY and UG, and had participant input as the random effect, and light intensity and measurement timepoint as fixed effects, with measurement timepoint dummy-coded with 'pre-adaptation' as the reference. For UY, the model suggested that there was no significant main effect of light intensity ($t(1157.99) = -0.94$, $p = .370$), but that there was a significant effect of 5-post measurement time ($t(11.23) = 7.17$, $p < .001$) and 60-post measurement time ($t(11.71) = -2.69$, $p = .020$), and that there was a significant interaction between 5-post measurement time and light intensity ($t(1158.00) = 13.44$, $p < .001$), and between the 60-post measurement time and light intensity ($t(1158.00) = 3.13$, $p = .002$). This was consistent with the idea of a shift in UY after adaptation which varied with the luminance transmission of the goggle filters. However, the finding that there was a significant shift in UY at the 60-post timepoint, and that this varied with the luminance transmission of the goggles, was unexpected. For UG, the model also suggested that there was no significant main effect of light intensity ($t(11.18) = -0.53$, $p = .605$), but did not find significant effects of the 5-post measurement time ($t(1086.83) = 1.84$, $p = .067$), or the 60-post measurement time ($t(1086.83) = -1.58$, $p = .115$). There was, however, a significant interaction between 5-post measurement time and light intensity ($t(1086.83) = 7.42$, $p < .001$), and between the 60-post measurement time and light intensity ($t(1086.83) = 2.64$, $p = .008$).Taken together, these results suggest that chromatic adaptation induced a light intensity-dependent shift in unique hues that was evident 5 minutes after adaptation and, unexpectedly, remained detectable 60 minutes later.

Based on the trend of the data as seen in Figure 3.9, it is likely that the significant interaction between light intensity and measurement time is driven by differences at the post-adaptation measurement point in both the UY and UG conditions. When the shift in unique hues between pre- and post-adaptation is plotted, the data seem to indicate a linear relationship, as can be seen in Figure 3.10. This was tested using a simple linear regression for UY and UG. The UY regression indicated a significant positive linear relationship ($F(1,38) = 26.16$, $p < .001$, R^2 *adjusted* = 0.39). The regression coefficient (B = 0.39, 95% CI[0.23,0.54]) suggested that an increase in one unit of light intensity would equate to an increase in unique yellow shift of 0.39 units. The UG regression also indicated a significant positive linear relationship ($F(1,35) = 17.99$, $p < .001$, R^2 *adjusted* = 0.32). The regression coefficient (B = 0.61, 95% CI[0.32,0.90]) suggested that an increase in one unit of light intensity would equate to an increase in unique green shift of 0.61 units.

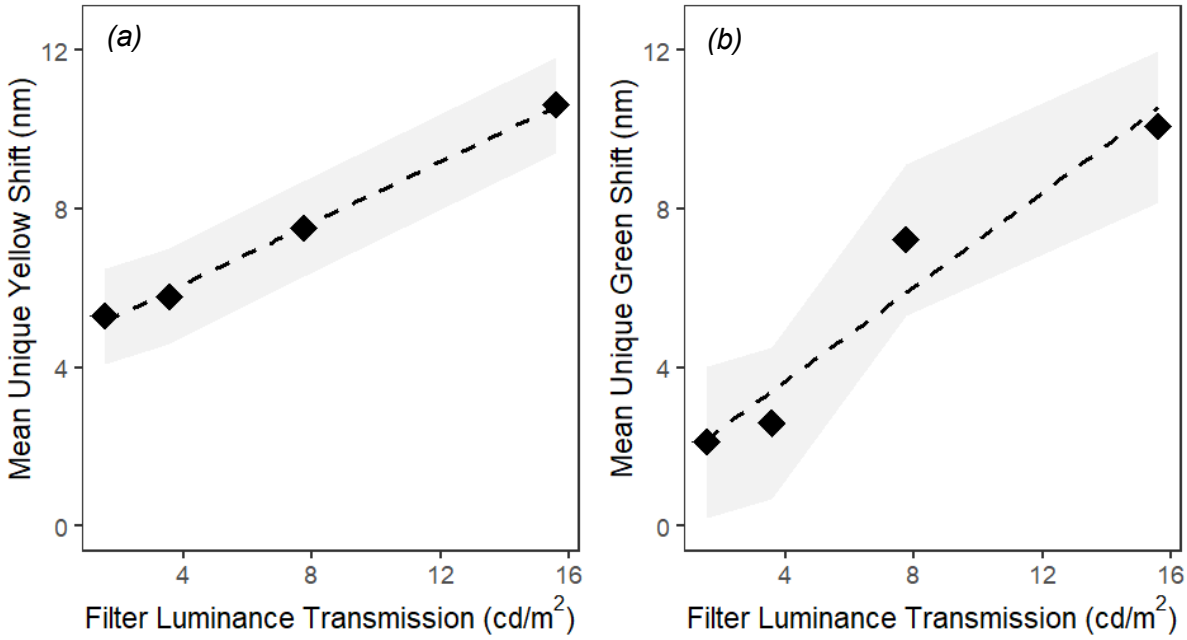


Figure 3.10: *Mean shift in a) unique yellow, b) unique green, at each level of filter luminance transmission. Lines indicate a linear model y~x fitted to the data. The shaded regions represent +/- one standard error of the mean.*

These findings indicate that the photometric luminance transmission of the filter has a large effect on the magnitude of the shift in unique hue settings following adaptation to a coloured filter. Does this indicate that the differences in unique yellow shift between the red and blue filters in Experiment 3.1 can be explained by the differences in luminance transmission between the filters? This can be tested by

extrapolating the trend in UY or UG shift as a function of filter luminance transmission, and calculating the predicted shift in UY/UG for a red filter of identical luminance transmission to the blue filter used. If filter luminance was the only factor causing a difference in the magnitude of aftereffect between the red and blue adaptation conditions in our first experiment, then we would expect the size of the UY shift to be the same in the blue condition as for a red filter of equal luminance transmission. A linear model based on the mean UY shifts as a function of filter luminance transmission gave the equation: $y = 4.55 + 0.39 * x$ to describe the relationship between luminance and size of UY shift (where x is the luminance of the filter – in this case, 0.77 cd/m^2). Based on this model, we would predict an equal luminance red filter to produce an average UY shift of -4.85nm compared to the observed average UY shift from the blue filter of -3.57nm. This suggests that the red filter had a slightly bigger effect on UY than the blue filter regardless of the differences in luminance transmission between the filters.

Similarly, the same technique can be applied to predict the shift in UG after adaptation to a red filter of equal luminance transmission to the blue filter. A linear model based on the UG data gave the equation: $y = 1.26 + 0.61 * x$ (where x is the luminance of the filter – in this case, 0.77 cd/m^2), which predicted a shift of -1.72nm compared to the observed average UG shift from the blue filter of -6.28nm. This suggests that the blue filter had a bigger effect on UG than the red filter regardless of the differences in luminance transmission. The comparison of predicted versus observed UY and UG can be seen in Figure 3.11.

(a)

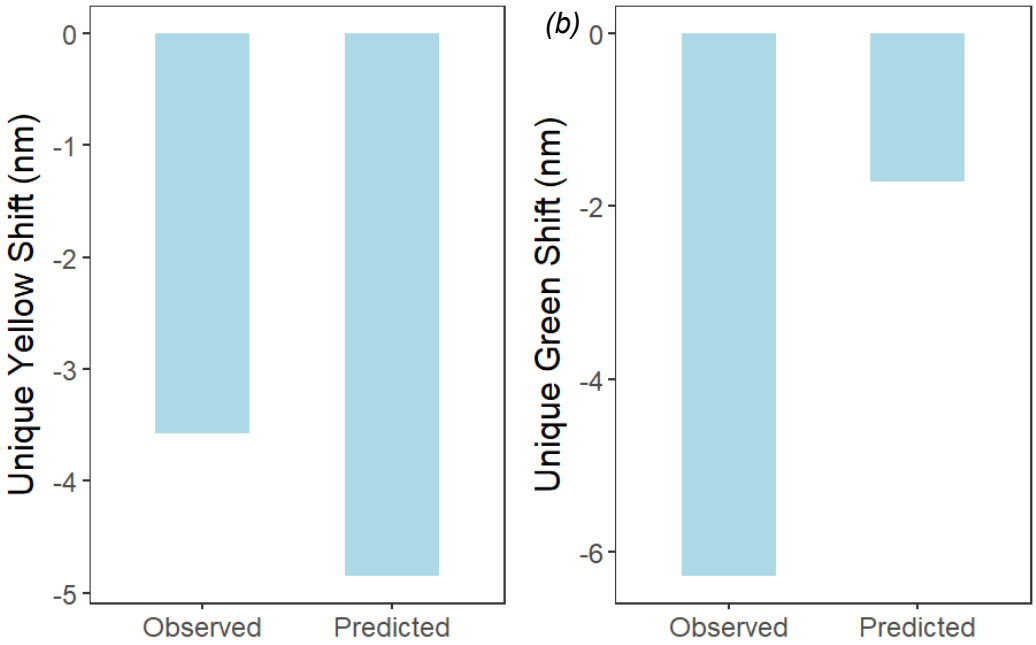


Figure 3.11: *Observed Unique Yellow shift (between pre- and 5-post measurement points) after 60 minutes adaptation to blue filter, versus predicted shift for a red filter of equivalent luminance transmission. B: Observed Unique Green shift (between pre- and 5-post measurement points) after 60 minutes adaptation to the blue filter, versus predicted shift for a red filter of equivalent luminance transmission.*

This suggests that the results of Experiment 3.1 do reveal real differences in the size of unique hue shifts after adaptation to red versus blue, and that the differences cannot be explained by discrepancies in the luminance transmission of the filters alone. However, we note that this model is limited in its linearity; at sufficiently high light levels, it would predict unrealistically large shifts in unique hues. It is inevitable that at very high or low light levels, the linear relationship modelled here would break down.

3.4 Modelling

One aim of this research was to establish a model of medium-term chromatic adaptation, in which we could predict the changes in the perception of unique hues from the wavelength transmission spectra of the adapting filter. The model presented here gives a prediction for changes in unique yellow depending on spectral characteristics of the adapting filter. It gives a theoretical maximum value of the shift of unique yellow, which can be used to quantify the percentage of the maximum shift achieved by an observer under certain conditions. The model is limited in that it does

not model the effects of changing the effects of light intensity or duration of adaptation.

In order to predict the changes in cone stimulation that would be caused by each filter, the spectral transmissions of each filter were measured, and are presented in the graph below. As can be seen in the graphs, the red filter primarily transmits light above 590nm, and the blue filter primarily transmits light below 490nm.

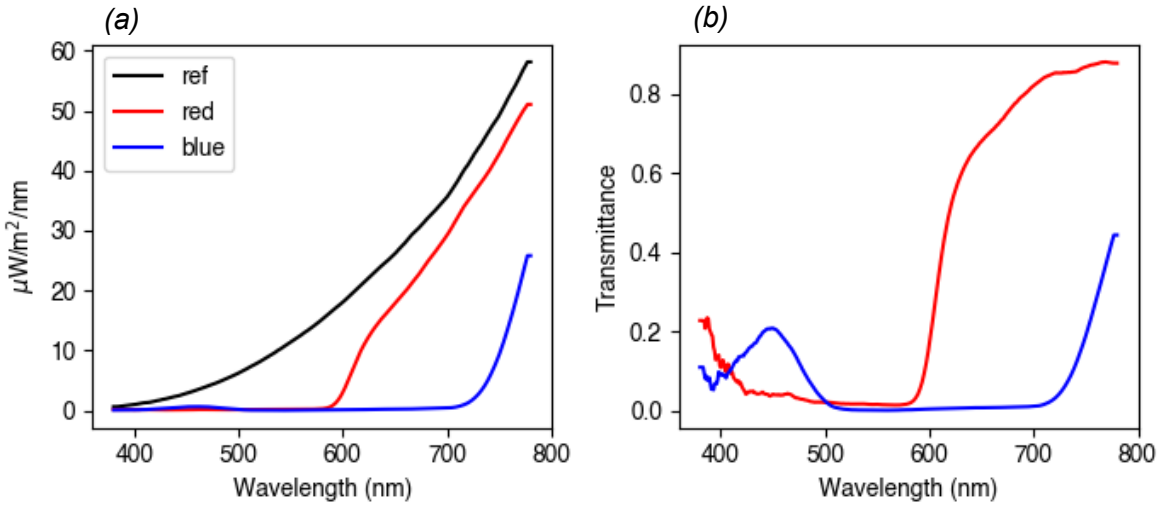


Figure 3.12: (a) *The spectral irradiance of the reference light source, and with the red and blue filters applied.* ***(b)*** *The calculated transmittance of the red and blue filters.*

Unique yellow was estimated as being determined by the L/M cone ratio. Unique yellow under equal energy white light was set as the average pre-adaptation UY settings of the participant group, which was 575nm. Stockman and Sharpe's (2000) cone fundamentals were used to determine a L/M cone ratio. These cone fundamentals were sampled at the same wavelengths as the measurements of filter transmittance. Next, a signal was computed from the cone fundamentals to give a L/M ratio curve for equal energy white light at each wavelength in the spectrum. To give a scaling factor for the red adaptation curve, the following calculation was performed:

$$(log10\ (10 *\ sum(L * red\ transmittances) - (log10(10 *\ sum(M * red\ transmittances))$$

Which subtracted the M cone sensitivities multiplied by the red filter transmittance from the L cone sensitivities multiplied by the red filter transmittance. This scaling factor was subtracted from the equal energy white curve for each wavelength.

The same calculation was performed to give a scaling factor for the blue adaptation curve:

$$(log10(10 * sum(L * blue\ transmittances) - log10(10 * sum(M * blue\ transmittances))$$

And this also subtracted from the white curve. This gave shifted L/M ratio curves for the conditions of the red filter and the blue filter.

These shifted curves can be used to predict the maximum adaptation possible to the filter; if there was to be a complete reweighting of L and M cones to adjust to the chromatically altered environment, the L/M ratio would be reweighted to match the calculated curve. The points on the red and blue curve where the L/M signal strength corresponds to the L/M signal strength for unique yellow on the white curve therefore correspond to the maximum possible shift in unique yellow to the adaptation conditions. This is represented in Figure 3.13, which shows that the maximum predicted UY shift for the red filter results in a UY value of 612nm (a shift of 37nm), and for the blue filter results in a UY value of 532nm (a shift of -43nm).

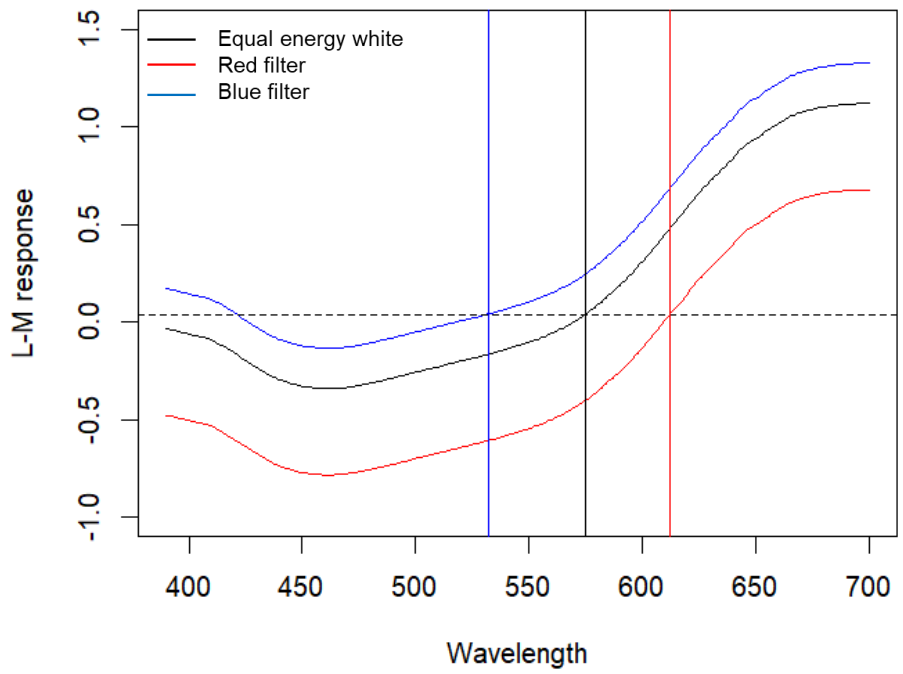


Figure 3.13: *L-M ratio for equal energy white light, the blue filter, and the red filter. The horizontal dashed line represents the L-M response equivalent to unique yellow. Vertical lines represent the predicted maximum unique yellow settings for each condition.*

The observed shifts in unique yellow for each condition and the percentage of the maximum shift they represent are shown in the tables below (Table 3.2 and 3.3).

Table 3.2: *Percentage maximum shift observed for unique yellow settings in each condition of adaptation duration after adaptation to red filters.*

Condition	Shift	Percentage
Red 15 minutes	6.01nm	16.25%
Red 60 minutes	9.51nm	25.71%
Red 240 minutes	10.55nm	28.52%

Table 3.3: *Percentage maximum shift observed for unique yellow settings in each condition of adaptation duration after adaptation to blue filters.*

Condition	Shift	Percentage
Blue 15 minutes	3.66nm	8.50%
Blue 60 minutes	3.59nm	8.31%
Blue 240 minutes	4.77nm	7.10%

The same method was used on each participant individually to model the predicted maximum shift for each participant, and the percentage of the maximum shift that was achieved by the adaptation at each duration of adaptation. One consideration for the large individual differences in the sizes of shift of UY observed between participants could be that observers are showing a similar amount of adaptation in terms of the relative shift towards an individual maximum, even if this results in different absolute sizes of UY shift between participants. However, the percentage of the maximum shift achieved by adaptation was found to also vary considerably between individuals, as shown in Figure 3.14, suggesting that this is not the explanation for individual differences in recorded adaptation strength.

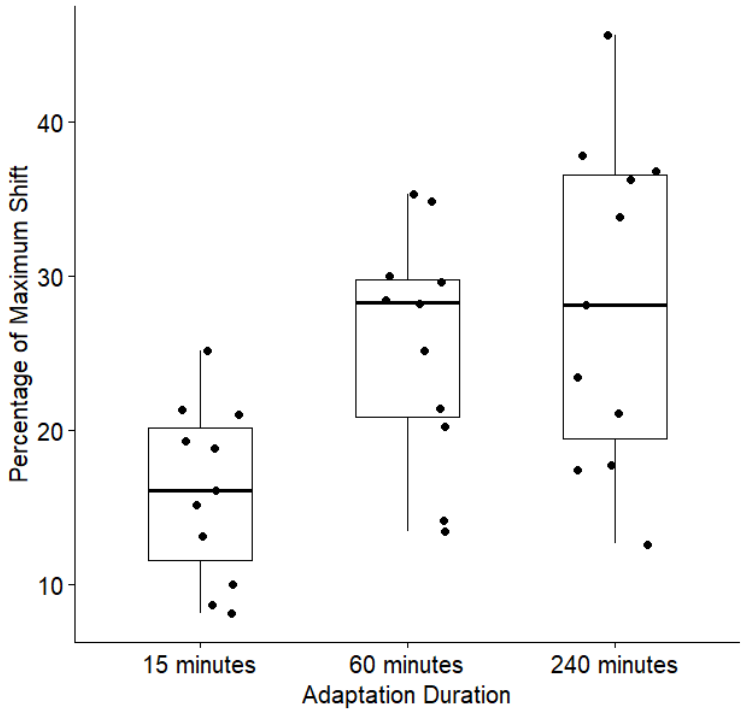


Figure 3.14: *Percentage of predicted maximum shift for each participant which was achieved after 15, 60, or 240 minutes of adaptation to a red filter. Each point represents a single participant.*

3.5 General Discussion

The results of these experiments suggest that the intensity and duration of an adapting environment both influence the magnitude of shifts in colour perception. They indicate a medium-term chromatic adaptation that increases with brighter and longer adaptation conditions, reaching a plateau between 15 and 60 minutes. It seems likely that this process would also show a plateau in sufficiently high intensity environments (as beyond a certain point the environment will be so bright as to maximise all cone output), although we did not achieve a high enough light intensity in this experiment to show this. The direction of the chromatic adaptation is determined by the wavelength spectrum of the adapting environment, with red environments causing previous settings of yellow to appear greener after removing the filter (therefore shifting unique yellow towards redder settings), and blue environments causing previous settings of yellow to look redder after removing the filter (therefore shifting unique yellow towards greener settings). The extent to which the perception of different unique hues is affected by the adapting environment also depends on the colour of the adapting environment, with yellow showing a greater shift after adaptation to red environments than blue environments.

The results of this study are consistent with some previous findings of the effects of medium-term adaptation. Li et al. (2020) also found that medium-term colour adaptation builds up over the course of 60 minutes. However, Shikamura and Sakata (2022) found that colour adaptation was complete within 10 minutes, and did not continue to build up over the course of an hour, with the strength of adaptation effects decreasing after the saturation point was reached. However, this may be due to the experimental setup, which involved adapting participants to a relatively weak yellow light that targeted only the peripheral retina. Our data would suggest that this would lead to a small ‘dose’ of the adapting stimulus, leading to small shifts in observers’ neutral points, and therefore these effects may decay faster than adaptation effects could accumulate. Using a stimulus with higher light intensity and broader spatial coverage may have led to stronger adaptation that continued to build across this time frame, as observed in the current study.

This ‘medium-term adaptation’, which builds over a longer timescale than the rapidly saturated photoreceptor response but does not persist as long as multi-day renormalisation, is in some ways inherently intuitive. Adaptation is known to occur at multiple levels of the visual system. Any information on global changes to the chromatic environment must be communicated to later stages of the visual system through the earlier stages of the visual system, with information on adaptation being repeated at multiple loci (Carandini & Heeger, 2012). This may be an optimal strategy, as multiple variations to the environment at different timescales can occur simultaneously (Kording, 2007). The results of our experiment may demonstrate medium-term adaptation that is engaged over a time period of a few minutes to a few hours, and which lasts for several minutes beyond the adaptive environment. Such a mechanism would be useful in our visual environment in adapting to global changes in chromaticity that last for several hours and may be briefly interrupted, such as changes in the weather. On a sunny day, for instance, it would be maladaptive to recalibrate colour perception dramatically when a single cloud passes overhead, but appropriate if the sky becomes consistently overcast.

One finding from Experiment 3.1 was that unique hue shifts were smaller after adaptation to the blue filter compared to the red filter. One initial explanation was that this difference related to the differences in the weighting of post-receptoral pathways, such as the L/M pathway, after adaptation to each colour. In the red condition, the effect of adaptation would be to decrease the gain of L cone signals relative to M cone signals, whereas in the blue condition, the effect of adaptation would be to decrease the gain of M cone signals relative to L cone signals, and with additional gain control of S cones. The red and the blue condition therefore changed the L/M ratio in opposite directions, which our model shows would predict different magnitudes of shift of unique yellow (although, notably, the model actually predicts a larger shift in the blue condition compared to the red condition, which was not found in the data. This may have been due to the influence of other post-receptoral pathways on the appearance of unique yellow, such as the S/(L+M) pathway, or other less canonical pathways such as the L/(L+M) pathway, modulating the effect in ways not fully captured by the model.)

However, a potential alternative explanation for the difference in unique hue shifts between the red and blue conditions in Experiment 3.1 was that the luminance transmission of the two filters was not matched: the red filters transmitted approximately four times more light than the blue filters. As a result, the smaller effect magnitudes observed in the blue condition may simply reflect reduced visual input driving the cones. However, the results of Experiment 3.2 show that while light intensity does influence the magnitude of unique hue shifts, it cannot fully account for the differences found in Experiment 3.1. Specifically, the unique yellow shifts in the blue condition were smaller than would be predicted for an equiluminant red filter, and the unique green shifts were larger than would be predicted for an equiluminant red filter. This suggests that some of the difference between the red and the blue condition may still be explained by differences in adaptation of cone-opponent pathways.

There has been some controversy over modelling unique hues as corresponding to post-receptoral pathways, such as considering unique yellow as the ‘null’ point of the L/M ratio. The concept of unique hues emerges from Hering’s theory of colour opponency (Hering, 1964), which considers that any colour can be described as a mixture of red versus green, blue versus yellow, or black versus white, and that therefore these colours must be perceptually privileged, and represented with some sort of physiological opponent mechanism. The theory was initially supported by hue cancellation experiments (Hurvich & Jameson, 1957), which showed that an amount of green can be added to red such as to ‘cancel out’ the redness, forming a colour that is uniquely yellow. The discovery of cone-opponent cells, corresponding to L/M opponent cells and S/(L+M) opponent cells was taken as further support for the hypothesis (Barlow, 1972). However, later research showed that the L/M and S/(L+M) axis (the cardinal axes) did not correspond to red/green and blue/yellow, but to somewhere perceptually in-between these colours (Webster et al., 2000). Furthermore, hue cancellation experiments have since been conducted which show that unique hue settings change depending on the prompt that participants are given (Bosten & Lawrance-Owen, 2014), suggesting that the concept of the unique hue may be linguistically dependent. Therefore, the cardinal colour contrast axes are not a direct correlate of our experience of unique hues, and unique hues cannot be explained by relative numbers of excited L- and M-cones or their sensitivities (Mollon

& Jordan, 1997). There is an obvious issue with considering unique yellow to be the 'null' point of a red-green channel if the red-green channel does not exist to begin with. Some suggestions have been made to address the difference between colour appearance and physiological colour pathways.

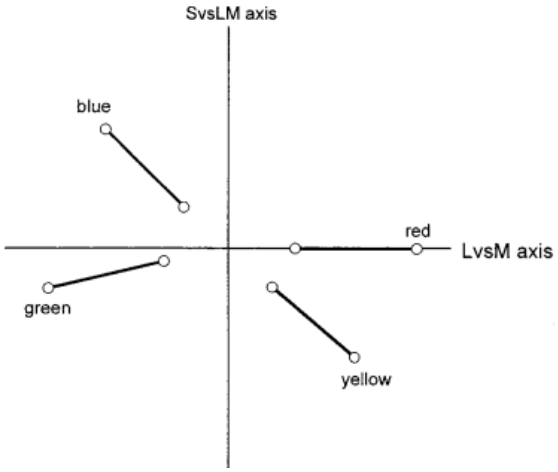


Figure 3.15: *Locus of unique hues in cone-excitation space for a single observer. Points plot the chromatic angles for unique red, green, blue, or yellow. From (Webster & Mollon, 1994)*

One suggestion is that there is a third recombination of cone signals at a point later than the LGN, and that this produces non-linear combinations resulting in our experience of colour being non-linear to the cardinal axes (De Valois & De Valois, 1993; Guth, 1991). However, Conway et al. (2023) put forward a compelling argument that unique hues are in no way perceptually privileged over other hues, and that the salience of unique hues may be solely cultural or linguistic. This paper suggests that 'unique' hues do not exist in an innate physiological sense, and instead suggests that the salience of colours emerges from experiencing the properties of a visual environment ('Utility-based coding'). This theory suggests that the way in which we perceive and describe colours is based on the colours surrounding us, and the way in which these are engaged with lexically. Conway explains: "*Utility-based coding stipulates that if some colors are special, their specialness should be attributed to meaningful structure in the world, structure that has utility. For example, unique yellow and blue might be understood not in terms of constraints imposed by encoding mechanisms but in terms of sun and sky – environmental features of universal relevance. Capturing meaningful structure must engage neural processes far beyond encoding because the relevant features might*

vary depending on context and behavioral goals." This is similar to previous suggestions that hues are learned based on variations in the visual environment, and that unique hues may represent an adaptation away from the cardinal axes (J. D. Mollon, 1982; Pokorny & Smith, 1977). While an interesting idea, this new theory makes it very difficult to conceptualise or model unique hues; for the purposes of this thesis, therefore, unique yellow is still modelled using the L/M pathway, but with the caveat that this may not be the most physiologically accurate model in light of recent theories in colour neuroscience.

Another possible cause for the differences between the red and blue conditions may be due to the role of S-cones. S-cones were suppressed to a much greater degree in the blue condition compared to the red condition. S-cones contribute far less to the overall retinal signal than L- or M-cones, due to there being fewer S-cones and fewer ganglion cells that have inputs from S-cones (Lee, 1999). S-cones have also previously been found to display slower responses to changes in light level, to have smaller changes in response to changes in background illumination, and to be generally noisier than L- or M-cones (Baudin et al., 2019). It is therefore possible that the S-cone dependent pathways have a smaller impact on determining dynamic colour perception than the L/M pathway. There is some support for this viewpoint; unlike Unique Yellow, which is stable across the course of the lifespan, Unique Green changes as a function of age, suggesting that S-cone dependent pathways are not flexibly adapting to the yellowing of the lens in the way that the L/M pathway adapts (J. S. Werner & Schefrin, 1993).

It is worth noting that when discussing the adaptation of cone pathways, that filters used in this experiment are unlikely to induce a 'pure' adaptation of one cone type, or one post-receptoral pathway, while leaving others unaffected. L and M cones retained some sensitivity in the blue condition, for example, although greatly suppressed, and so may have displayed some adaptation. Likewise in the red condition, S cones were not 100% suppressed. This leads to some ambiguity in the results. For example, although there was a smaller UY shift in the blue condition than predicted for an equiluminant red condition, there still was a shift in UY, which may be due to the residual sensitivity of L and M cones in this condition; without being perfectly suppressed, there may have been altered gain control of the L/M pathway

as well as the S/(L+M) pathway. However, it is arguably impossible to achieve perfect targeting of cone pathways in this set up with naturalistic filters; to achieve it would require silent substitution calculations.

In conclusion, these studies found that shifts in unique hues in the direction of adaptation to a chromatically-altered environment are maintained five minutes after adaptation, and decay back to baseline within one hour. This suggests that this may be a medium-term adaptation process that occurs on a timescale and at a locus between that of rapid photoreceptor adaptation, and long-term cortical renormalisation. It is potentially part of a continuum of adaptation processes that allow us to simultaneously adapt to changes in the colour of our environments at multiple timescales. It was also found that shifts in unique yellow settings were larger after adaptation to red, and had a longer period of change before plateauting, compared to shifts in unique yellow settings after adaptation to blue. Luminance transmission differences between the filters were found to account for some, but not all, of the differences in magnitude of unique hue shift between the red and the blue adaptation conditions. Finally, we present a model of optimal adaptation to the filters used and suggest that the extent to which the visual system achieves this optimal adaptation depends on the ‘dose’ of the adapting environment, determined by its duration and luminance.

Chapter 4: Adaptation Recovery After Medium-Term Adaptation

Adaptation recovery is informative about the processes that might be underlying adaptation. In the previous chapter, unique hues were measured 60 minutes after removing the filtered goggles, and it was found that there was no significant difference between settings of unique hues between pre-adaptation and this 60-minute post-adaptation point. In this chapter, in Experiment 4.1, we considered that reducing the post-adaptation measurement point to 30 minutes may allow some adaptation effects to be captured (as predicted by the decay by trial analysis in Chapter 3, and a pilot study measuring unique yellow settings at different stages of recovery). However, there were no significant differences between unique hue settings in the 30- and 60-minute post-adaptation conditions.

Another avenue for exploration is the passivity of the adaptation recovery process. Short term colour adaptation is not preserved by keeping observers in darkness, unlike other adaptation effects such as motion aftereffects, which are cortical in origin (Spigel, 1960a). Thus, the absence of 'storage' may be because short term colour adaptation occurs retinally rather than cortically. One way in which to test whether medium term adaptation occurs cortically may be to test whether adaptation effects are 'stored' when observers spend the recovery period in darkness, rather than in the light. In Experiment 4.2, six participants adapted to red for an hour, then spent a 45-minute recovery period either in normal daytime illumination, or in complete darkness. It was found that in both conditions, participants' unique yellow settings returned to pre-adaptation levels after the recovery period.

4.1 Introduction

As well as the immediate effects of adaptation on colour perception, an equally informative source of information can be the endurance of the aftereffects of adaptation after exposure to the visual environment has ceased. It is the persistence of changes in colour perception over hours, days, or even months back in normal illumination conditions that has led researchers to previously suggest that long term

adaptation must be occurring at a post-retinal point in the visual system (e.g. Delahunt et al., 2004). Because of the assumption that retinal adaptation mechanisms are unlikely to adapt for long periods of time (perhaps due to the necessity of maintaining sensitivity to react to very short-term changes in the chromatic environment), this means that the rate of decay of adaptation effects is of interest. Slower decay may suggest that a later stage of the visual system is adapting (Jameson & Hurvich, 1979). As briefly mentioned in the previous chapter, the finding that adaptation effects were not present 60 minutes after adaptation may suggest that adaptation effects are happening at an early stage of the visual system. However, the effects still being present five minutes after adaptation suggests this may not be rapid photoreceptor adaptation, as this is thought to decay within five minutes (Rinner & Gegenfurtner, 2000).

The decay in adaptation effects after short term adaptation is well-documented. Wright (1946) performed a series of experiments involving adapting participants to red, green, or blue stimuli of different intensities (900, 1800, 3600, 7200 photons). Participants were adapted in one eye for 180 seconds, then the adapting stimulus was briefly removed, and participants were asked to match an orange stimulus (610nm) that was presented in the unadapted eye. Cycles of top-up adaptation and testing periods continued until participants were happy with the match. Participants then continued to make matches with the test colour across the next 150 seconds. Wright used this matching data to plot recovery of red and green sensitivity across the 150 seconds after adaptation. Brighter intensities of the adapting stimulus led to a slower recovery of red and green sensitivity. In another series of experiments, Jameson et al. (1979) showed that five minutes of adaptation caused large shifts in unique hues that decayed rapidly back to baseline within five minutes. However, they also showed that alternating adaptation with blackness, such that observers received five minutes of adaptation spread across 10 minutes, caused a smaller shift in unique hues that decayed slower, suggesting that the duration of the adaptation period also has an effect on rate of decay. This evidence gives us, so far, two factors that affect rate of adaptation decay: the intensity of the initial adaptation, and the duration of the period of adaptation. It may be possible to elicit a shift in perception that endures for longer after adaptation to an environment in some conditions, even in the absence of a difference in the initial size of the shift. This may indicate that

longer term mechanisms of adaptation were being engaged. Therefore, one way to investigate the strength of adaptation is to measure differences in the rate of decay of adaptation effects, as well as the initial shift.

Another factor which could affect the rate of adaptation recovery is the visual environment present during the recovery process. The effects of short-term adaptation decay regardless of whether observers spend the recovery period receiving visual input or not. Adapting for short periods of time is followed by a decay in adaptation effects even when observers spent the time between tests in the dark (Jameson and Hurvich, 1979). However, adaptation that must be occurring in the cortex is often maintained by a lack of visual input, and is thought to need active de-adapting stimulation to cause the adaptation effects to decay. For example, motion aftereffects can be extended in duration by participants closing their eyes after exposure to the adapting stimulus (Culham et al., 1999; Spigel, 1960b). This adaptation must be cortical, as retinal neurons cannot detect motion.

Within the realm of colour, it has been suggested that a similar process may account for the endurance of the McCollough effect. The McCollough effect is an orientation-dependent colour aftereffect caused by viewing alternating orthogonal gratings comprising coloured lines and black lines. The colours are usually selected to differ categorically, e.g. red (vertical) and green (horizontal). The chromatic aftereffect is only seen when the observer then looks at a stimulus that consists of a black and white grating of the same orientation (McCollough, 1965). For the example given, therefore, the red vertical adaptation leads to a green aftereffect for vertically oriented black and white gratings and vice versa for a horizontally oriented black and white grating. The aftereffect is very long-lasting – only 10 minutes of adaptation can cause aftereffects for up to 24 hours (Jones & Holding, 1975). One suggestion for the reason that this aftereffect is so persistent is that it may be stored until the visual system is presented with a de-adapting stimulus. As it is relatively rare to view striped stimuli of a specific orientation in our day-to-day life, the effect persists for longer than other aftereffects, where de-adapting stimulation is constantly present (Vul et al., 2008). The McCollough effect is also suggested to be caused by cortical adaptation, as orientation-selective neurons only appear from V1 onwards.

The literature therefore suggests that adaptation occurring at early stages of the visual system is not ‘stored’ in the absence of de-adapting visual input, but cortical adaptation is. Therefore, one measure to determine the locus of adaptation could be to see whether it is maintained by the absence of visual input during the adaptation recovery period. If the adaptation effect is ‘stored’ during recovery in the dark, we can suggest that it is occurring in the cortex.

In Experiment 4.1, participants adapted to red-filtered goggles of different luminances for one hour. Unique hues were measured both 30 and 60 minutes after the filtered goggles were removed. It was hypothesised that there may be shifts in unique hues present after 30 minutes of recovery in the brighter luminance conditions, but not the darker.

In Experiment 4.2, participants adapted for one hour to a red filter, then spent the duration of the post-adaptation ‘recovery’ period in a completely dark room rather than in normal illumination. We hypothesised that there may be a smaller recovery in unique hues back to baseline in this condition compared to when participants recovered in normal illumination.

4.2 Experiment 4.1: Recovery of adaptation effects after adaptation to red filters of different luminance.

As well as adapting participants to red environments of different light intensities, in this experiment, participants were also split into two recovery groups; one group that was tested at 30 minutes recovery and one group that was tested at 60 minutes recovery. Wright’s data (1946) suggest that short term adaptation to higher intensities of light causes larger changes in colour perception that take longer to recover (as seen in Figure 4.1), and as we predicted larger adaptation effects for higher light intensities, it was predicted that this may also lead to more enduring adaptation effects.

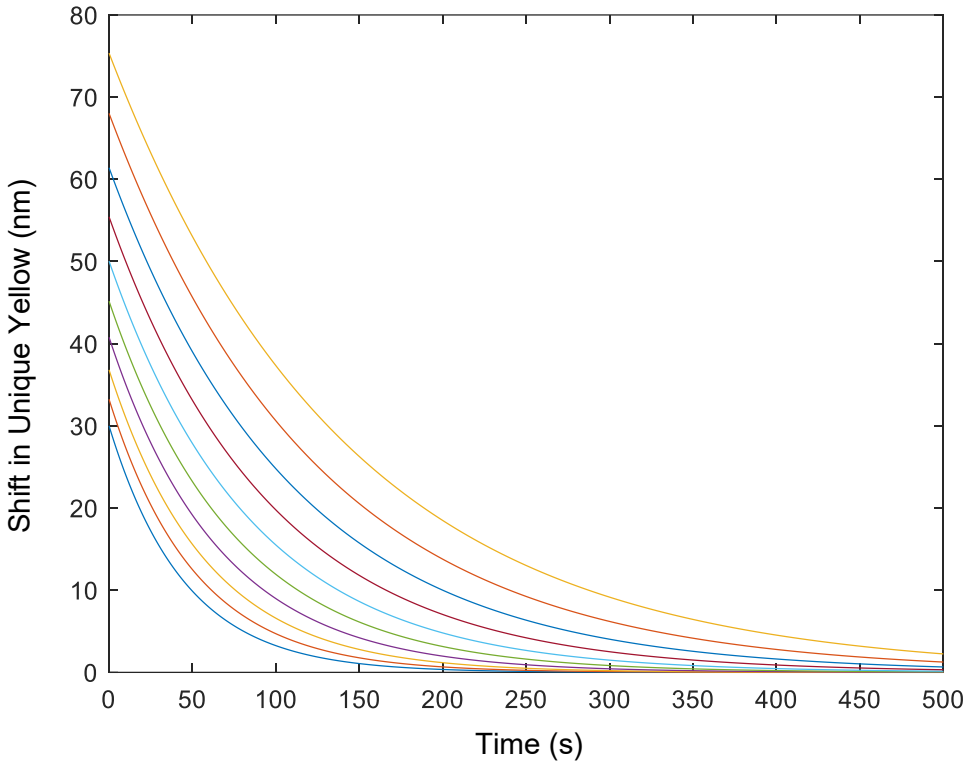


Figure 4.1: *Rendering of adaptation decay for unique yellow settings after 180s adaptation to a red stimulus. Lines represent intensities of adapting stimulus from 700 photons to 7200 photos. Calculated from recovery curves of red and green sensitivity reported by Wright, 1934. Credit: Antony Morland, 2023.*

In the previous chapter, we modelled predictions of how long it would take unique yellow settings to return to pre-adaptation settings. These predictions suggested that, after adaptation to red, unique yellow settings should return to baseline around 40 minutes after the 5-post adaptation measurement point. This suggested that the effects of one hour of adaptation would cease to be detectable around 45 minutes post-adaptation, and may still be able to be detected before this point.

A pilot experiment adapted four participants for one hour to the red goggles with the highest luminance transmission and measured their UY settings at either 0, 15, 30, or 45 minutes after removing the goggles. These initial data (Figure 4.2) suggested that adaptation decayed over the course of the 45 minutes, with a detectable shift at 30 minutes post-adaptation but not at 45 minutes post-adaptation. Based on these data, it was considered that 30 minutes post-adaptation would be a suitable point for comparison; under brighter conditions, there should be a detectable effect, but under dimmer conditions, there may not be.

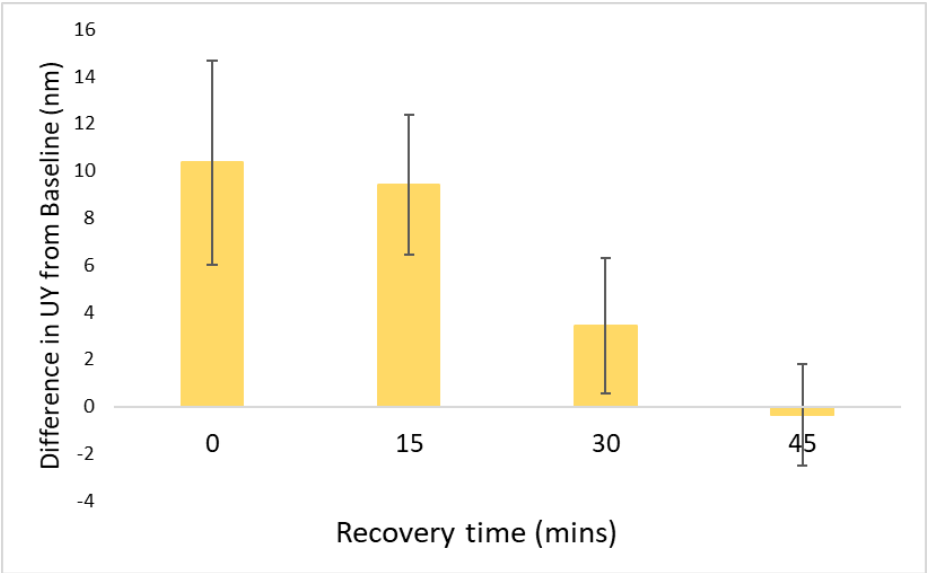


Figure 4.2: *Unique Yellow settings after 60 minutes adaptation to red goggles and 0-, 15-, 30-, or 45-minutes recovery time. Each recovery time point was measured in a single participant. Error bars represent standard deviation.*

4.2.1 Methods

The methods reported here have already been reported in Chapter 3. However, for ease of reference, they are reiterated here.

Participants

10 participants took part in this experiment (2 male, 8 female, 5 naïve, 5 non-naïve). All participants took part in all four testing conditions, but for 3 participants who had previously participated in the 1-hour red adaptation condition, their data from this experiment were used for the no-luminance-filter condition, as the experimental protocol was the same. Participants gave their consent for this data to be reused.

Participants were aged between 18-60 and were colour-normal observers as assessed by Rayleigh matching. Informed consent was obtained in accordance with the University of York Department of Psychology Ethics Committee.

Design

We used a within-subjects design in which the within-subjects factor was luminance levels during adaptation (of which there were four levels). Outcome measures were unique hues.

Apparatus

Participants were adapted using goggles filtered with Lee acrylic filters, as in the previous experiment (see Chapter 3 for a summary of the spectral transmissions of the goggles and their effects on cone sensitivity.) In addition to the red Lee filter, three of the goggles also had neutral density filters applied, the luminance transmissions of each are in Table 4.1.

Table 4.1: *Luminance transmission of each pair of goggles used in the experiment.*

Filter	Luminance transmission (cd/m^2)
Red filter (No neutral density filter)	15.596
Red filter + neutral density filter Lee 209	7.764
Red filter + neutral density filter Lee 210	3.578
Red filter + neutral density filter Lee 211	1.566

Unique Hues measurement

Monochromatic light (subtending .67° x 1.33° visual angle) was presented via a tristimulus colorimeter (Wright, 1928, 1931) and altered using the method of adjustment. For unique yellow measurements, participants were instructed to turn a dial that shifted the stimulus wavelength along a monochromatic spectrum. Instructions were given to set Unique Yellow (UY) and Unique Green (UG) by instructing participants to stop the dial when the stimulus appeared neither red nor green, or neither more yellow nor more blue. Starting points along the monochromatic spectrum were randomly selected, and it was alternated whether the starting point tended towards longer or shorter wavelengths on the spectrum relative to the range of unique hue settings. Participants made 11 UY judgments in each session and their average UY was calculated from the last 10 UY settings. The same method was applied to Unique Green measurements. Measurements were taken in a dark room.

Procedure

Participants remained in the red-filtered environment for 60 minutes. Before each testing session, participants were dark-adapted for five minutes. Participants' unique hue and Rayleigh Match settings were tested at three time points: before wearing the goggles (pre-adaptation), 5 minutes after removing the goggles (post-adaptation), and either 30 or 60 minutes after removing the goggles.

Statistical Analysis

Results were analysed using three-way mixed model ANOVAs with follow-up analyses using one-way ANOVAs and post-hoc t-tests. These analyses were performed in R, and the ANOVAs were performed using the afex package. Bayes Factor analyses were also run, in order to be able to verify the presence or absence of reliable effects. These were performed using JASP.

4.2.2 Results and Discussion

The pre-, 5-post-, and long-post adaptation wavelength settings for unique yellow (UY) and unique green (UG) for each level of filter luminance transmission are plotted in Figure 4.3. These data suggest that there is little difference between the pattern of UY or UG settings at any measurement timepoint between the 30- and 60-minute recovery conditions.

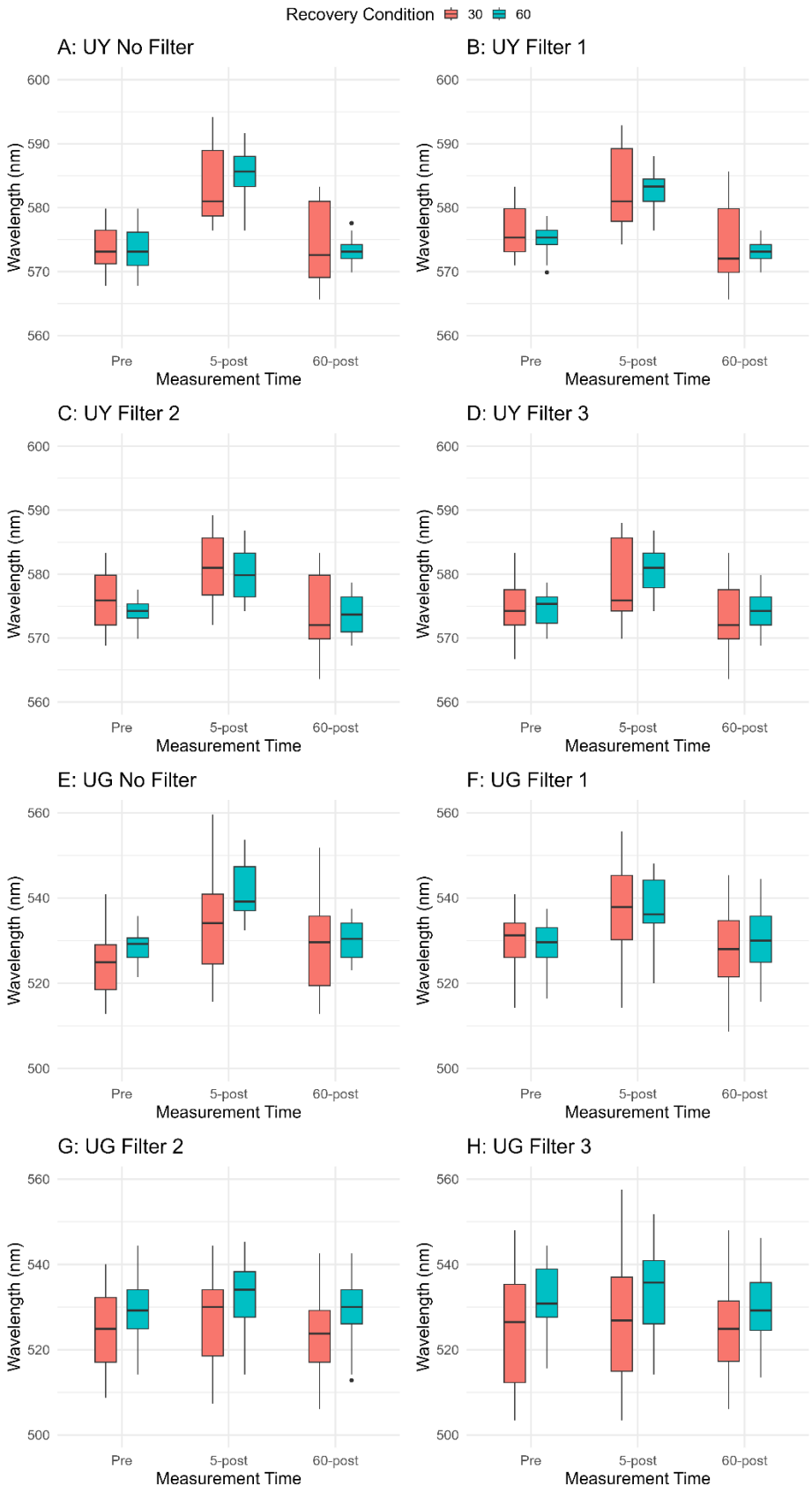


Figure 4.3: *Comparison of unique hue settings in the 30-minute recovery vs the 60-minute recovery adaptation conditions for unique yellow (a-d) and unique green (e-h) for each filter luminance level.*

Two three-way mixed model ANOVAs were conducted to analyse the unique yellow (UY) and unique green (UG) long-post adaptation settings across each level of filter luminance transmission. The within-subjects factors were light intensity (no filter, filter 1, filter 2, filter 3), and measurement timepoint (pre-, 5-post-adaptation, and long-post), the between-subjects factor was recovery group (30 or 60 minutes), and the outcome measure was the unique hue tested.

For unique yellow, the ANOVA suggested that there was no significant interaction between the amount of recovery time and the light intensity ($F(3,24) = 9.25$, $p = .444$), nor was there a significant interaction between recovery time and the measurement timepoint ($F(2,16) = 1.33$, $p = .292$), nor was there a significant three-way interaction between recovery time, light intensity, and measurement timepoint ($F(6,48) = 3.99$, $p = .876$), nor was there a significant main effect of recovery time ($F(1,8) = 1.00$, $p_{\lambda} = .922$). This indicated that there was no significant difference between the recovery time groups, and that this lack of significant difference did not alter based on the light intensity condition, the settings made at other timepoints, or both the light intensity and the settings made at other timepoints.

For unique green, the ANOVA suggested that there was no significant interaction between the amount of recovery time and the amount of light in the adapting environment ($F(3,15) = 1.07$, $p = .393$), nor was there a significant interaction between recovery time and the measurement timepoint ($F(2,10) = 0.07$, $p = .931$), nor was there a significant three-way interaction between recovery time, light intensity, and measurement timepoint ($F(6,30) = 0.71$, $p = .641$), nor was there a significant main effect of recovery time ($F(1,5) = 0.82$, $p = .407$). This indicated that there was no significant difference between the recovery time groups, and that this lack of significant difference did not alter based on the light intensity condition, the settings made at other timepoints, or both the light intensity and the settings made at other timepoints.

In order to confirm the lack of difference between the 30-minute and 60-minute recovery conditions, we ran a Bayes Factor independent samples t-test on the 30-minute and 60-minute post adaptation time points. These suggested there was no

difference between 30-minute post-adaptation and 60-minute post-adaptation unique yellow settings (BF_{10} = 0.32), and no difference between 30-minute post-adaptation and 60-minute post-adaptation unique green settings (BF_{10} = 0.62).

These results suggest that in all light intensity conditions, perception of unique hues was not significantly different from pre-adaptation settings within 30 minutes of recovery, and the greater intensity of adaptation in the higher light intensity conditions did not cause adaptation aftereffects to be more likely to be detected at 30-minutes post-adaptation than the lower light intensity conditions, contrary to predictions.

4.3 Experiment 4.2: Adaptation Recovery in Dark versus Light Environments

4.3.1. Methods

Subjects

Six participants who had already taken part in the red condition from the previous experiment (see previous chapter) also participated in the red adaptation dark recovery condition (2 male, 4 female, 5 naive, 1 non-naive). Data was compared to the 60-minute red adaptation condition described in the previous chapter. All participants had previously taken part in this condition. Participants gave their consent for this data to be reused.

Participants were aged between 18-60 and were colour-normal observers as assessed by Rayleigh matching. Informed consent was obtained in accordance with the University of York Department of Psychology Ethics Committee.

Design

We used a within-subjects design in which the within-subjects factors were light during recovery (light or dark), and measurement time (pre, 5-post, and 60-post). The outcome measure was unique yellow.

Apparatus

Participants were adapted using red goggles filtered with Lee acrylic filters, as in the previous experiment.

The dark room was found to have no detectable ambient light (as measured by a Minolta photometer).

Unique Hues and Rayleigh Match

Unique hues and Rayleigh Matches were measured using a Wright colorimeter. The same method of recording unique hues was used as described in the previous chapter, but only unique yellow was measured.

Procedure

Participants remained in the red-filtered environment for 60 minutes. While wearing the goggles, they were told to continue their day normally. After removing the goggles, participants then spent 45 minutes in a completely dark room as a recovery period. Before the first two testing sessions, participants were dark-adapted for five minutes. Participants' unique hue and Rayleigh Match settings were tested at three time points: before adaptation, 5 minutes and 60 minutes post-adaptation.

Statistical Analysis

Results were analysed using two-way repeated measures ANOVAs using the afex package in R. Bayes Factor analyses were also run, in order to be able to verify the presence or absence of reliable effects. These were performed using JASP. Consistent with previous experiments, linear mixed effect models were run using the lme4 and lmerTest packages in R.

4.3.2. Results and Discussion

The condition in which participants spent the recovery period in darkness rather than in the light was compared to the data from the 60-minute adaptation duration light recovery condition only for the participants who had participated in both conditions of the experiment. These data are illustrated in Figure 4.4. A two-way repeated measures ANOVA with factors of measurement time (pre-adaptation, 5-post, and 60-post) and recovery condition (light and dark) showed no significant interaction

between measurement time and recovery light (F(2,10) = 0.31, p = .739), nor was there a main effect of recovery light significant (F(1,5) = .03, p = .867), though as would be expected, the main effect of measurement time was significant ($F(2,10) = 56.72$, $p < .001$). This suggested that adaptation aftereffects recover to the same extent after 60 minutes when participants are exposed to light and when they remain in darkness. In order to quantify the evidence for this null hypothesis, we ran a paired Bayes Factor t-test, comparing the 60-post unique yellow settings in the light and dark recovery conditions. This suggested there was no difference between the two conditions ($BF_{10} = 0.46$).

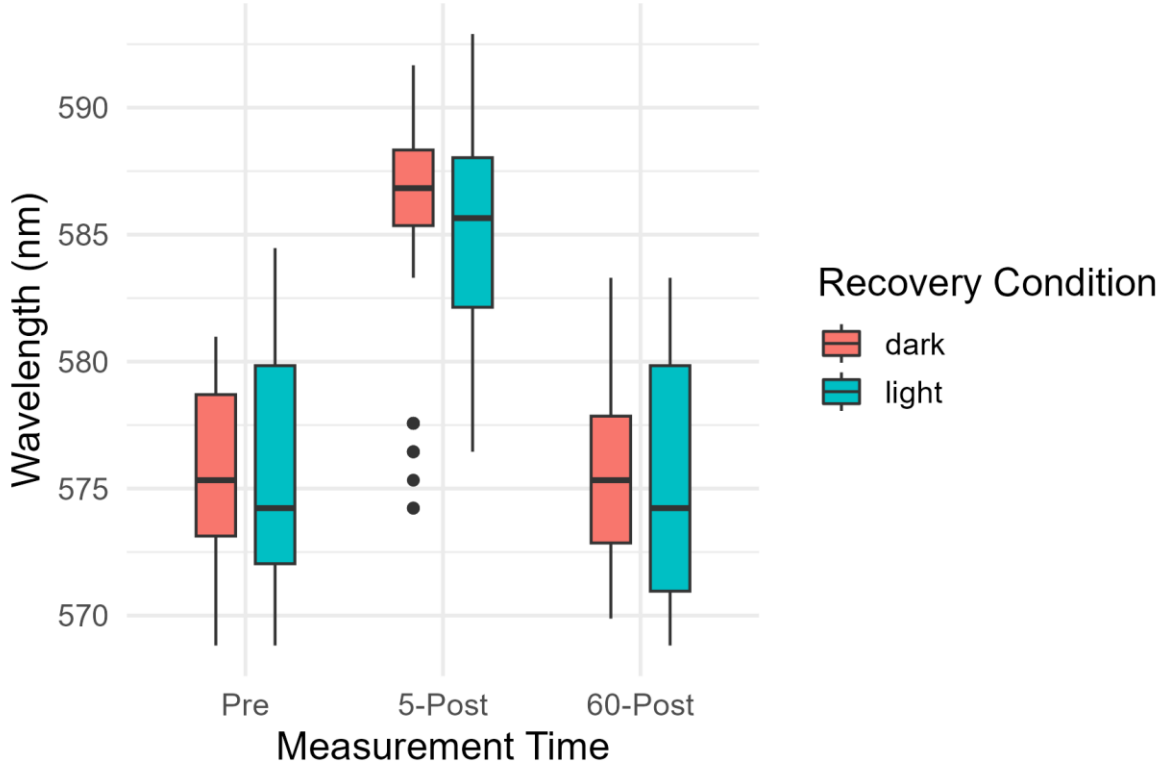


Figure 4.4: *Unique Yellow settings pre-adaptation, post 1-hour adaptation, and post-recovery, where recovery was either spent in complete darkness or normal illumination.*

As in the previous adaptation experiments, in order to incorporate within-subject variation, linear mixed-effects models were run on the entire dataset, including all trials from all participants. Participants were input as random effects, and measurement time (pre, 5-post, 60-post) and light level during recovery as fixed effects. Measurement time was dummy-coded with pre-adaptation as the reference

level. Recovery light level was also dummy-coded as a factor with ‘light’ as the reference level.

The model showed a significant change in UY settings from pre to 5-post adaptation ($t(5.12) = 6.42$, $p = .001$), but no significant difference between pre and 60-post adaptation ($t(8.48) = -1.52$, $p = .165$). There was no significant main effect of recovery light level ($t(339) = -1.15$, $p = .252$), nor was there a significant interaction between recovery light level and the 5-post timepoint ($t(339) = 1.41$, $p = .161$), or between recovery light level and the 60-post timepoint ($t(339) = 1.85$, $p = .066$). This corroborated the results of the ANOVA.

The results of this experiment suggest that there is no difference between unique yellow settings one hour after adaptation, regardless of whether the recovery period is spent in the dark or in the light. This suggests that the recovery of chromatic adaptation at this timescale is a passive process, in which adaptation trends back to an internal baseline setting regardless of whether there is visual input representing that chromatic environment or not.

4.4 General Discussion

The results of these investigations into the unique hue settings during the post-adaptation period after adapting to a red filter suggest a fairly rapid recovery process, which is complete within 30 minutes of removing the filtered goggles, and is not preserved by darkness during the recovery period. This suggests that this adaptation may be happening at an early stage of the visual system, probably pre-cortical, due to the evidence that cortical adaptation may endure for longer (e.g. the McCullough Effect), and be preserved by darkness (e.g. motion aftereffects). Given the evidence from Shikamura & Sakata (2022) that adaptation can transfer from the periphery to the fovea, this suggests that this type of ‘medium term’ adaptation may be occurring in post-receptoral cone-opponent pathways, either in the eye or the LGN.

The results of Experiment 4.1 differ from our predicted time course for adaptation recovery after adaptation to a red filter, based on the trial-by-trial differences at the 5-post adaptation measurement point (see 3.2 Experiment 3.1: Time course of

adaptation at different durations and chromaticity of environments). The observed results suggested that adaptation returned to pre-adaptive settings faster than was predicted. There are a few potential explanations for this. Firstly, participants may simply have displayed a smaller magnitude of adaptation in this experiment by chance. A smaller magnitude of adaptation is associated with faster recovery (Wright, 1946). However, this was not the case; in this experiment, participants showed a marginally larger mean shift in unique yellow (10.62nm in Chapter 4 Experiment 4.1, [one hour, red, no neutral density filter], compared to 9.51nm in Chapter 3 Experiment 3.1, [one hour, red, no neutral density filter]). A second explanation could be that there may have been differences in the recovery environments, with perhaps the mean illumination being brighter in the experiment reported in this chapter. However, although this was not measured, the results from Experiment 4.2 suggest that lower light intensities in the recovery environment are unlikely to preserve adaptation aftereffects, so this explanation is unconvincing. A more likely explanation is that adaptation recovery is non-linear, and therefore the linear model used to predict the rate of recovery did not completely accurately predict the pattern of recovery. A final explanation may be that the presence of the test stimulus itself interfered with the recovery of adaptation during the testing period, leading to a shallower slope, however, this is difficult to effectively measure. An alternative testing paradigm may be to only ask participants to make a single unique yellow setting at each measurement point in order to reduce the effect of the test stimulus on colour perception. However, this approach requires many repeated trials in order to account for natural variability in unique yellow settings, which would necessitate multiple sessions of adaptation and adaptation recovery. This is possible for short durations of adaptation, but understandably difficult to achieve for long durations of adaptation and adaptation recovery.

Considering the results of Experiment 4.2, the lack of difference between unique yellow settings after recovery in the dark or light is suggested to indicate a passive recovery process. However, this does not definitively rule out the involvement of cortical mechanisms. It could be that the adaptation is cortical, but not ‘stored’ for as long as the recovery period. The point at which unique hues return to baseline during the recovery period is not known and may vary considerably for different individuals. Testing 60 minutes after adaptation only probes a point at which recovery is already

complete when the recovery period is spent in the light. The results of Experiment 4.1 further suggest that recovery may be complete, or at least, sufficiently complete that effects can no longer be detected, within 30 minutes post-adaptation. Therefore, in order for there to be a detectable adaptation effect 60 minutes post-recovery, storage effects caused by darkness during recovery would need to increase the duration of the aftereffect by over 100% for it to be detected. As such, it can only be concluded that there is no 100% increase in the endurance of adaptation aftereffects. This is not an improbable increase to have expected (Jameson and Hurvich (1979) found that interspersing the adaptive stimulus with periods of darkness increased the duration of adaptation effects by 100%), however, it also cannot be ruled out that darkness may have had a smaller but still meaningful impact on the duration of adaptation effects in this study. A more sensitive study may compare unique hue settings at a range of points during the recovery period during a light and a dark recovery period, in order to investigate whether there is a more subtle increase in the duration of adaptation effects.

Furthermore, colour adaptation is driven directly by cone photoreceptors, and in the dark, cone photoreceptors become hyperpolarised (Nakatani & Yau, 1988). This may mean that any cortical adaptation mechanisms act as though stimulated even in darkness, and may be actively de-adapted even in the absence of light. This further supports the argument that while evidence of storage of colour adaptation in the dark can be used to support the idea that the mechanism is cortical and needs active de-adaptation, the absence of evidence does not necessarily mean that the mechanism is pre-cortical or passive.

Overall, the conclusions that we can draw from this pattern of results are limited. While the results provide some evidence for the idea that medium term colour adaptation recovery, like short term colour adaptation recovery, is a passive process that decays back to an internal norm, the caveats make it difficult to be certain of this. The only thing that we can conclude is that lack of visual input certainly does not perfectly store chromatic adaptation; if it does slow the rate of decay at all, this is likely to be a small effect.

Chapter 5: Binocular Interactions in Chromatic Adaptation

One psychophysical method of investigating whether an adaptation effect occurs cortically is to measure whether the adaptation effect transfers between the eyes. As information from the eyes is first combined in primary visual cortex, the existence of interocular transfer effects is strong evidence for adaptation in binocular cells in visual cortex. Previous studies of interocular transfer in chromatic adaptation have generally occluded the non-adapted eye, potentially causing binocular suppression. In this chapter, participants are adapted binocularly or dichoptically to luminance-matched red or blue filters in two studies. Unique yellow settings are measured from both eyes, or just the non-dominant eye, before and after adaptation. No significant interocular transfer of adaptation effects is observed. This may indicate a pre-cortical site for colour adaptation, however, alternative explanations are also considered.

5.1 Introduction

The structure of the visual system means that signals between each of the eyes are first combined in the visual cortex, with V1 being the first area that shows evidence of binocularly tuned neurons (Hubel & Wiesel, 1979). Many adaptation paradigms, for example, adaptation to motion or orientation, adapt these binocular neurons. One effect of this is that presenting an adaptive stimulus in one eye causes the aftereffect to also be observed in the non-adapted eye, a phenomenon known as interocular transfer. Because earlier stages of the visual system only have monocular inputs, this interocular transfer can be used as a marker that an adaptation effect is occurring at a cortical level; in V1 or at a later stage of the visual system. This can therefore be used as a psychophysical technique to probe whether colour adaptation is occurring at a cortical stage, or at an earlier stage of the visual system before the combination of signals across the eyes.

There is mixed evidence as to whether chromatic adaptation transfers between the eyes. Some evidence reports changes in colour in the non-adapted eye following

dichoptic adaptation, but only a small number of participants have been tested, and findings are variable. Webster and Mollon (Webster & Mollon, 1994) tested for threshold changes in the non-adapted eye in a dichoptic adaptation experiment (using asymmetric temporal variations in chromaticity around a mean chromaticity) for two observers, and found that one observer displayed weak aftereffects in the non-adapted eye that aligned with the direction of adaptation, while the other observer displayed non-directionally specific adaptation aftereffects in the non-adapted eye. This paper also reports that Krauskopf et al. (1982), and Chan et al. (1986) found evidence of sensitivity changes in the non-adapted eye following adaptation to a red-green grating (however, these papers are no longer accessible to be able to confirm this). Kaufman et al. (1981b) showed that the McCollough effect could transfer interocularly when participants were exposed to diffuse white light in their unadapted eye, rather than the unadapted eye being occluded. Favreau & Cavanagh (1983) also showed interocular transfer to spatial frequency using equiluminant gratings that differed only in their chromaticity, suggesting that colour contrast can drive spatial frequency adaptation that transfers between the eyes. One commonality between these experiments is that the adapting stimulus had a spatial or temporal component as well as a chromatic component, which may have helped to drive cortical changes.

In terms of ‘pure’ chromatic adaptation, in which participants adapt to a change in the global hue of an environment, without adaptation being contingent on structural properties of the environment, the evidence seems to suggest that interocular transfer does not occur. Eisner and Enoch (1982) reported that after one week’s adaptation to a monocular red filter, there was no shift in sensitivity in the unadapted eye, whereas there was a substantial shift in the adapted eye, when tested 30 minutes after the red filter was removed. Delahunt et al., (2004) show that the neutral point of cataract patients, which shifts after the removal of the cataract, does not change in the eye without the cataract. Only one study reports interocular transfer of long-term chromatic adaptation (Neitz, 2002). However, these studies all also have a commonality; in each study, interocular transfer was only tested for in a single participant. It is difficult to draw conclusions about interocular transfer in long term adaptation from so little data across studies which use different methodologies and measurements.

It may be questioned whether interocular transfer of colour adaptation should be predicted even if it is cortical. Some views suggest that there is no binocular integration of colour signals in V1, and that colour pathways remain monocular until a later stage. However, this has been largely disproven by the discovery of colour-sensitive neurons in V1 that respond to input from both eyes (Peirce et al., 2008). Furthermore, optical imaging suggests that interocular transfer effects may be present in monocular neurons as well as binocular neurons, possibly due to lateral inhibition (Howarth et al., 2009). This would suggest that even if colour signals are primarily processed by monocular neurons in the brain, we should still expect to see some degree of interocular transfer of colour aftereffects if they are occurring at a cortical level.

One explanation for discrepancies in interocular transfer findings could be differences in the binocular integration of colour information between different studies. A methodological difference between two studies that had contradictory findings on interocular transfer was whether the unadapted eye was occluded, or exposed to normal illumination (Neitz et al, 2002; Eisner & Enoch, 1982). Both of these designs have potentially large implications on interocular transfer. Occluding one eye disrupts ocular dominance, and can lead to a reduced sensitivity of the patched eye (Lou et al., 2011) and may lead to inhibitory interactions which suppress the occluded eye (Chadnova et al., 2017). Supporting this, White et al (White et al., 1978) show evidence for interocular transfer of the McCullough effect when the non-adapted eye is shown a diffuse white field, but not when the non-adapted eye is occluded. On the other hand, exposing one eye to normal daylight illumination may also cause rivalry and inhibition between the eyes, rather than integration. The daylight environment will naturally be brighter than the colour-filtered environment, and may become dominant. It has been found that when the luminance differs between the two eyes, the eye with the lower luminance exerts less suppression over the other eye (Ding & Levi, 2017). This may lead to a prediction that adaptation in the filtered eye would not affect the unadapted eye due to its lower luminance.

In this experiment, observers were adapted to two filters that were equivalent in luminance, but differed greatly in colour. This created a large difference in chromatic

environment between the eyes, which allowed for large effect sizes that could be sensitive to small binocular effects, but did not have the confounding factors associated with occlusion or exposure to normal daylight. Although dichoptic chromatic environments may result in binocular rivalry, which could cause inhibition of interocular effects, this can be reduced by ensuring that the luminance and structure of the environment is matched between the eyes. Studies of discrimination thresholds have shown that wavelength discrimination is worse when each eye is presented with a different colour, suggesting that there is interocular interference in the discrimination of colour, and therefore that colour fusion of dichoptic colours does occur (Sagawa, 1982). Furthermore, dichoptic viewing of different colours can induce binocular colour mixture, in which a third colour is seen which is a combination of the two colours. This can occur regardless of stereo-rivalry between the two eyes and takes time to build up (Erkelens & van Ee, 2002), which is further suggestive that binocular colour mechanisms fuse chromatic environments between the eyes. This evidence leads to the prediction that if chromatic adaptation occurs in binocular cells, then dichoptic adaptation should lead to an alteration in colour perception.

There were three possible predictions for the effect of adapting to dichoptic chromatic environments. If adaptation is purely monocular, then the size of the shift of unique hues in each eye after dichoptic adaptation to red or blue should be equivalent to the shift after binocular adaptation to the same colour. If adaptation is entirely binocular, then the adaptation to red and blue in each eye should ‘cancel out’, leading to a small shift in unique hues in the direction of the stronger adaptation. If adaptation is occurring in both monocular and binocular populations, however, then the size of the shift in unique hues after dichoptic adaptation should be smaller than after binocular adaptation, but in the same direction, as the adaptation in each eye ‘cancels out’ the other only to a small degree. These predictions are illustrated in Figure 5.1.

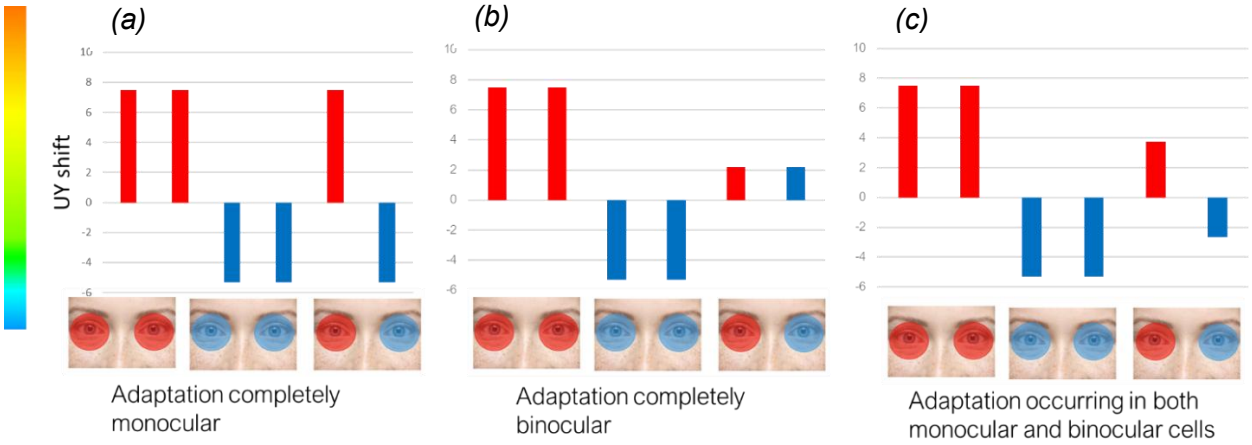


Figure 5.1: *Predictions for the direction of unique yellow shifts if adaptation effects are dependent on different levels of contribution of binocular cells. A) Predictions for unique yellow shift if adaptation effects rely on monocular populations, B) Predictions for unique yellow shift if adaptation effects rely on binocular populations, C) Predictions for unique yellow shift if adaptation effects rely on a mixture of binocular and monocular populations.*

5.2 Experiment 5.1: Binocular versus Dichoptic Adaptation to Red and Blue Environments

5.2.1. Methods

Participants

13 participants took part in this experiment (3 male, 10 female, 10 naïve, 3 non-naïve). All participants took part in all testing conditions.

Participants were aged between 18-60 and were colour-normal observers as assessed by the FM100 colour vision test. Informed consent was obtained in accordance with the University of York Department of Psychology Ethics Committee.

Design

The design was within-subjects, in which the within-subjects factor was the colour condition of adaptation (binocular red, binocular blue, dichoptic red-blue). Outcome measures were unique hues.

Apparatus

Participants were adapted using goggles filtered with Lee acrylic filters, as in the previous experiment (see Chapter 2 for a summary of the spectral transmissions of the goggles and their effects on cone sensitivity (2.2. Filter Measurements)). A neutral density filter was used to match the luminance of the red and blue filters.

Unique Hues measurement

Participants adjusted the wavelength of a coloured patch of light until it appeared 'uniquely yellow' (neither red nor green). Participants made 10 settings with each eye, alternating the eye that made the colour judgement. The eye that was not making the colour judgement was either closed or occluded with an eyepatch, depending on what participants found more comfortable. The same technique for setting unique hues on a colorimeter was used as in previous chapters (see 3.2.1 Methods).

Procedure

Participants remained in the colour-filtered environment for 60 minutes, during which time they watched a greyscale computer screen, in order to reduce binocular rivalry. Participants' unique hue settings were tested before and after adaptation to the binocular red, binocular blue, or dichoptic red-blue goggles, with five minutes of dark adaptation before each testing session. For the dichoptic red-blue goggles, six participants wore the red filter on their left eye, and seven participants wore the red filter on their right eye.

Statistical Analysis

Results were analysed using Greenhouse Geissner-corrected three-way mixed model ANOVAs with follow-up analyses using two-way ANOVAs. These analyses were performed in R, and the ANOVAs were performed using the afex package. Consistent with previous experiments, linear mixed effect models were run using the lme4 and lmerTest packages in R.

5.2.2 Results and Discussion

The results of this experiment showed, as shown in previous chapters, that adapting binocularly to red caused a shift towards redder hues of unique yellow (UY), and adapting binocularly to blue caused smaller shifts of UY towards greener hues. After adapting dichoptically to red and blue, most participants still showed a shift in UY settings in each eye according to the adaptation colour of that eye (i.e., the red-adapted eye shifted towards redder settings and the blue-adapted eye shifted towards greener settings). This can be seen in Figure 5.2.

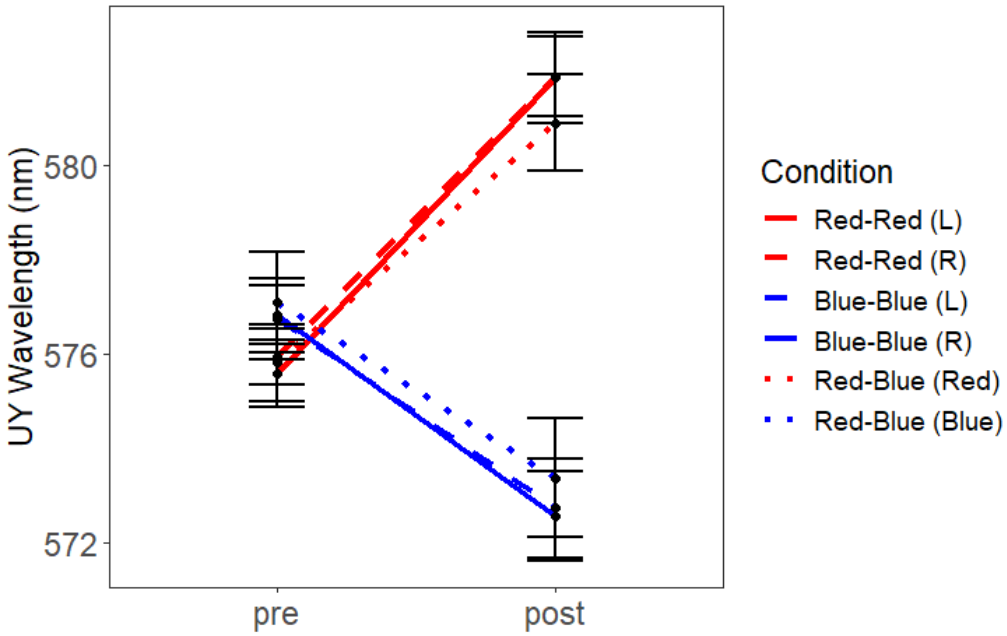


Figure 5.2: *Pre- and 5-post adaptation unique yellow settings in each eye after binocular adaptation to red, binocular adaptation to blue, or dichoptic adaptation to red and blue. Error bars represent +/- one standard error of the mean. For the binocular adaptation, the eyes shown are left (L) or right (R). For dichoptic adaptation, the eyes shown are red- or blue-adapted.*

These results were analysed using a three-way repeated measures ANOVA, in which the within-subjects factors were eye measured (Eye 1 or Eye 2: in the binocular conditions these were simply the left or right eye, but in the dichoptic condition eyes were split by whether they were adapted to red or blue[1]), the colour condition (red-red, blue-blue, or red-blue), and the measurement timepoint (pre-

[1] It was necessary to treat the eyes separately in the analysis in the binocular adaptation condition in order to ensure a consistent number of observations in the red-red condition compared to the red-blue condition.

adaptation or post-adaptation). We found a significant interaction between eye measured, measurement time, and condition ([GG] $F(1.23, 14.75) = 75.38$, $p < .001$, $\eta^2 = .09$).

As we had expected significant interactions in this analysis due to the opposite direction of effect after adaptation to red and blue, to follow up we performed two two-way ANOVAs, splitting the data into a red adaptation group and a blue adaptation group. The red ANOVA therefore had two within-subjects factors, adaptation eye condition (red-red left eye, red-red right eye, red-blue red eye) and measurement time (pre-adaptation and post-adaptation), and the blue ANOVA also had the factors of adaptation eye condition (blue-blue left eye, blue-blue right eye, red-blue blue eye), and measurement time (pre-adaptation and post-adaptation). The results of the red ANOVA showed no significant interaction between adaptation eye condition and measurement time ([GG] $F(1.34, 16.03) = 1.23$, $p = .300$), and no main effect of adaptation eye condition ([GG] $F(1.46,17.54) = 0.29$, $p = .681$), though there was a significant main effect of measurement time ($F(1,12) = 275.32$, $p < .001$). The results of the blue ANOVA showed the same pattern, with no significant interaction between adaptation eye condition and measurement time ([GG] $F(1.24,14.91) = 0.42$, $p = .571$), and no significant main effect of adaptation eye condition ([GG] $F(1.11,13.28) = 0.29$, $p = .62$), but a significant main effect of measurement time ($F(1,12) = 73.26$, $p < .001$). This pattern of results suggests there are significant shifts in unique yellow when measured post-adaptation compared to pre-adaptation, but that there is no effect of adapting binocularly versus dichoptically to either red or blue on the shift in unique yellow settings between these measurement points. The shifts in unique yellow settings in each eye in each condition are shown in Figure 5.3, which illustrates that the shifts in UY settings for each eye are not smaller in the dichoptic condition compared to the binocular conditions.

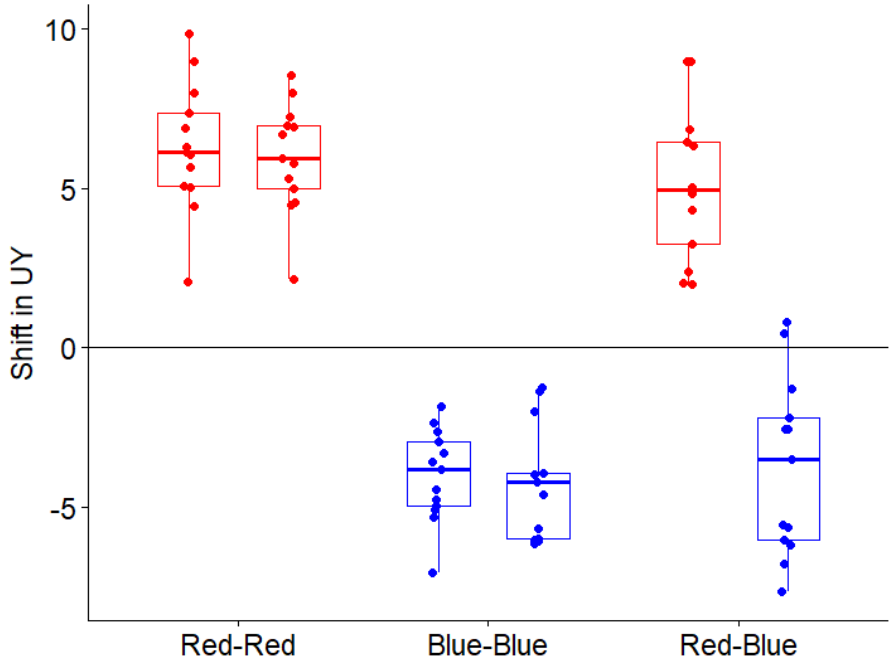


Figure 5.3: *Shift in unique yellow settings (between pre- and 5-post adaptation) in each eye, for the red binocular, blue binocular, and red-blue dichoptic adaptation conditions. These can be compared to the predictions made in Figure 5.1.*

However, settings were considerably more variable between participants after dichoptic adaptation, as can be seen from the spread of the data in Figure 5.3. Many participants showed smaller shifts in both the red and blue conditions when adapting dichoptically rather than binocularly, and although the effect did not reach significance, the mean shift in UY was smaller after dichoptic adaptation to red compared to binocular adaptation to red, and similarly, was smaller after dichoptic adaptation to blue, compared to binocular adaptation to blue.

In order to investigate whether within-participant variability had an impact on the results, and to maintain consistency with the other experiments, we ran a linear mixed effects model on the entire dataset. Participants were entered as random effects, while measurement time, colour condition, and eye measured were input as fixed effects with dummy-coded reference levels of pre-adaptation, blue-blue, and left eye (or the red eye, in the red-blue condition) respectively.

The model showed a significant main effect of measurement time on unique yellow settings, ($t(37.24) = -9.16$, $p < .001$), indicating that unique yellow settings were

significantly different at the post-adaptation timepoint compared to the pre-adaptation timepoint. There was also a significant main effect of the red-red colour condition, where the red–red condition differed significantly from the reference blue–blue condition, ($t(25.34) = -2.35$, $p = .027$). However, the red–blue condition did not differ significantly from the blue–blue condition, ($t(17.14) = -0.55$, $p = .589$). No significant main effect of eye measured was observed, ($t(61.38) = 0.25$, $p = .806$).

There were significant interactions between measurement time and both colour conditions. The interaction between measurement time and the red–blue condition was significant, ($t(1488) = 20.84$, $p < .001$), as was the interaction between measurement time and the red–red condition, ($t(1488) = 23.02$, $p < .001$), indicating that changes in unique yellow settings from pre- to post-adaptation differed as a function of colour condition. A significant three-way interaction was observed between measurement time, colour condition, and eye measured for the red–blue condition, ($t(1488) = -13.57$, $p < .001$), indicating that the time-dependent effect of the red–blue condition on unique yellow settings differed between the red and blue-adapted eye. No corresponding three-way interaction was observed for the red–red condition, ($t(1488) = -0.13$, $p = .898$), and no other two-way interactions involving eye measured reached significance (all ps > .56). These results corroborate the results of the ANOVA.

5.3 Experiment 5.2: Binocular versus Dichoptic Adaptation to Red Environments

This second experiment was functionally very similar to the previous experiment (5.1), and aimed to replicate the results, but had some differences in experimental design which will be outlined here. Primarily, this experiment aimed to control for a potential influence of ocular dominance by testing only the non-dominant eye.

5.3.1. Methods

Participants

17 participants took part in this experiment (3 male, 14 female). All participants took part in all testing conditions.

Participants were aged between 18-60 and were colour-normal observers as assessed by Rayleigh Matching. One participant was excluded from analysis due to having abnormal colour vision. Informed consent was obtained in accordance with the University of York Department of Psychology Ethics Committee.

Design

The design was within-subjects, in which the within-subjects factor was the colour condition of adaptation (binocular red, dichoptic red-blue). Outcome measures were unique hues.

Apparatus

Participants were adapted using goggles filtered with Lee acrylic filters, as in the previous experiment (see Chapter 2 for a summary of the spectral transmissions of the goggles and their effects on cone sensitivity (2.2. Filter Measurements).) A neutral density filter was used to match the luminance of the red and blue filters. The red filter was always presented to the non-dominant eye and the blue filter to the dominant eye in the dichoptic condition.

Unique Hues measurement

The same method of recording unique yellow was used as described in the previous experiment (see 5.2.1. Methods), however, participants' unique hues were only tested in their non-dominant eye (which was always red-adapted).

Procedure

Participants remained in the colour-filtered environment for 60 minutes, during which time they watched a greyscale computer screen. Participants' unique hue settings were tested before and after adaptation to the binocular red or dichoptic red-blue goggles, with five minutes of dark adaptation before each testing session. Only one eye - the non-dominant eye, which was red-adapted - was tested in each condition.

Statistical Analysis

Two-way repeated measures ANOVAs were performed on the average UY settings using afex in R. These were run for the individual dataset collected in this

experiment, and for the combined dataset across both experiments. However, due to only having access to participants' average UY settings for experiment 5.2, a linear mixed effect model was unable to be performed for this combined data.

Correlations between the UY shifts for each participant in different conditions were calculated using the cor function in R. The weakness of the correlation of UY shift magnitude between the red-red and red-blue conditions gave rise to the possibility that different groups of participants may be adapting in different ways, giving a similar mean shift, but comprising of distinct subgroups. This was tested with a linear mixed effect classifier, using the mclust package in R, based on the Bayesian information criteria.

5.3.2. Results and Discussion

The results of this experiment showed a shift in unique yellow settings towards longer wavelengths after adaptation to red. Similar to the results of the previous experiment (5.1), a two-way ANOVA suggested there was no significant interaction between measurement time (pre- or post-adaptation) and the adaptation condition (red-red or red-blue), ($F(1,15) = 3.21$, $p = .093$), no significant main effect of adaptation condition ($F(1,15) = 3.56$, $p = .079$), but a significant main effect of measurement time ($F(1,15) = 130.49$, $p < .001$). Surprisingly, there was actually a slightly greater mean shift in unique yellow after the dichoptic adaptation to red compared to the binocular adaptation to red, as can be seen in Figure 5.4, however, as the differences between the conditions were not significant, this may be spurious.

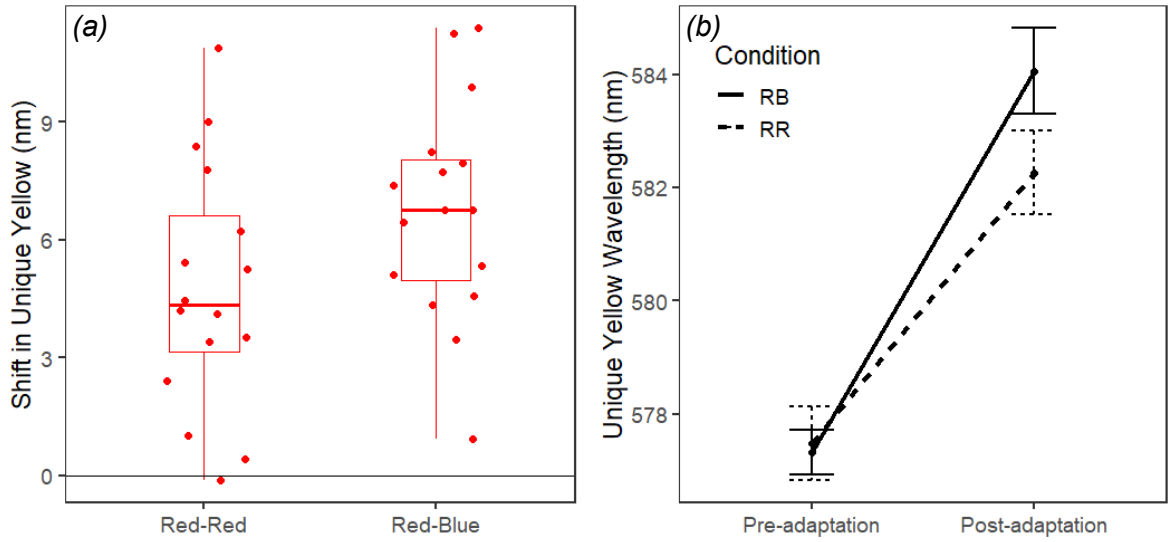


Figure 5.4: a) *Mean shift in unique yellow settings between pre- and post-adaptation measurement timepoints when measured in the non-dominant red-adapted eye in the binocular red or dichoptic red-blue adaptation conditions.* ***b)*** *The unique yellow settings made in the pre- and post-adaptation measurement timepoints in the binocular red or dichoptic red-blue conditions. Error bars represent standard error.*

These data were combined with the data from the right-eye red-red binocular condition and red-eye red-blue dichoptic condition in Experiment 1 (as excluding for the controls for ocular dominance, these otherwise used identical methodologies) to give the greatest statistical power. These combined data are shown in Figure 5.5. The combined results of all 29 participants were analysed in a two-way repeated measures ANOVA with factors of condition (red-red or red-blue), and measurement time (pre-adaptation or post-adaptation). The results corroborate the pattern observed in the smaller sample, with no significant interaction between measurement time and adaptation condition ($F(1,28) = 0.84$, $p = .366$), and no significant main effect of adaptation condition ($F(1,28) = 0.19$, $p = .668$), but a significant main effect of measurement time ($F(1,28) = 320.10$, $p < .001$).

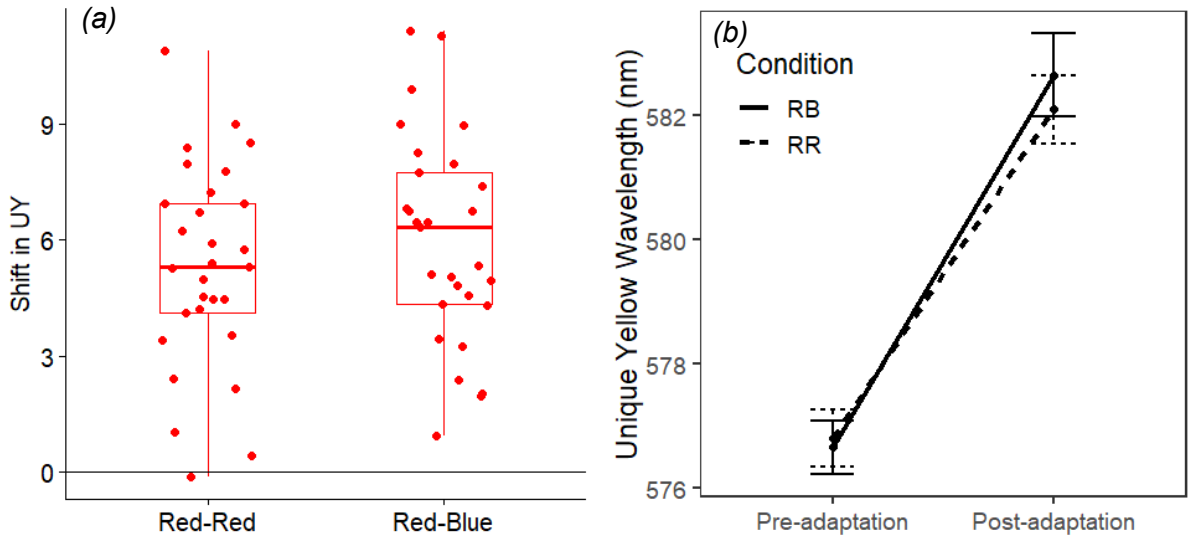


Figure 5.5: a) *Unique yellow settings made by either the right eye or red eye (Experiment 5.1) or the non-dominant eye (Experiment 5.2) in the red-red or red-blue adaptation conditions. Each point represents a single participant.* ***b)*** *Unique yellow settings at the pre-adaptation and post-adaptation measurement points in the right eye or red eye (Experiment 5.1), or the non-dominant eye (Experiment 5.2) in the red-red or red-blue adaptation conditions. Error bars represent standard error.*

We also investigated trends in unique yellow shifts for a red-adapted eye between the red-red adaptation condition and red-blue adaptation condition within individual participants. Based on findings from the previous chapters, we would anticipate medium to strong positive correlations between participants' unique yellow shifts in the red-red and red-blue adaptation conditions. However, this was not found in either Experiment 5.1 or Experiment 5.2 in this chapter. In Experiment 5.1, there was a weak negative correlation (r = -.23), and in Experiment 5.2, there was no correlation (r = - .08). When looking at the patterns of individual participants, it is clear that some participants were adapting far more in the red-blue condition than the red-red condition, while others were adapting more in the red-red condition than the red-blue condition. If there were no difference between the UY shifts in the red-adapted eye after red-red versus red-blue adaptation, then we would expect all the lines in Figure 5.6 to be flat, however, there are a considerable number that are not. The statistical test may have failed to find a significant effect because there is not a consistent trend across all participants, but instead, potentially different patterns within different groups of participants which could be explained by identifying sub-groups of participants who have similar patterns between the conditions.

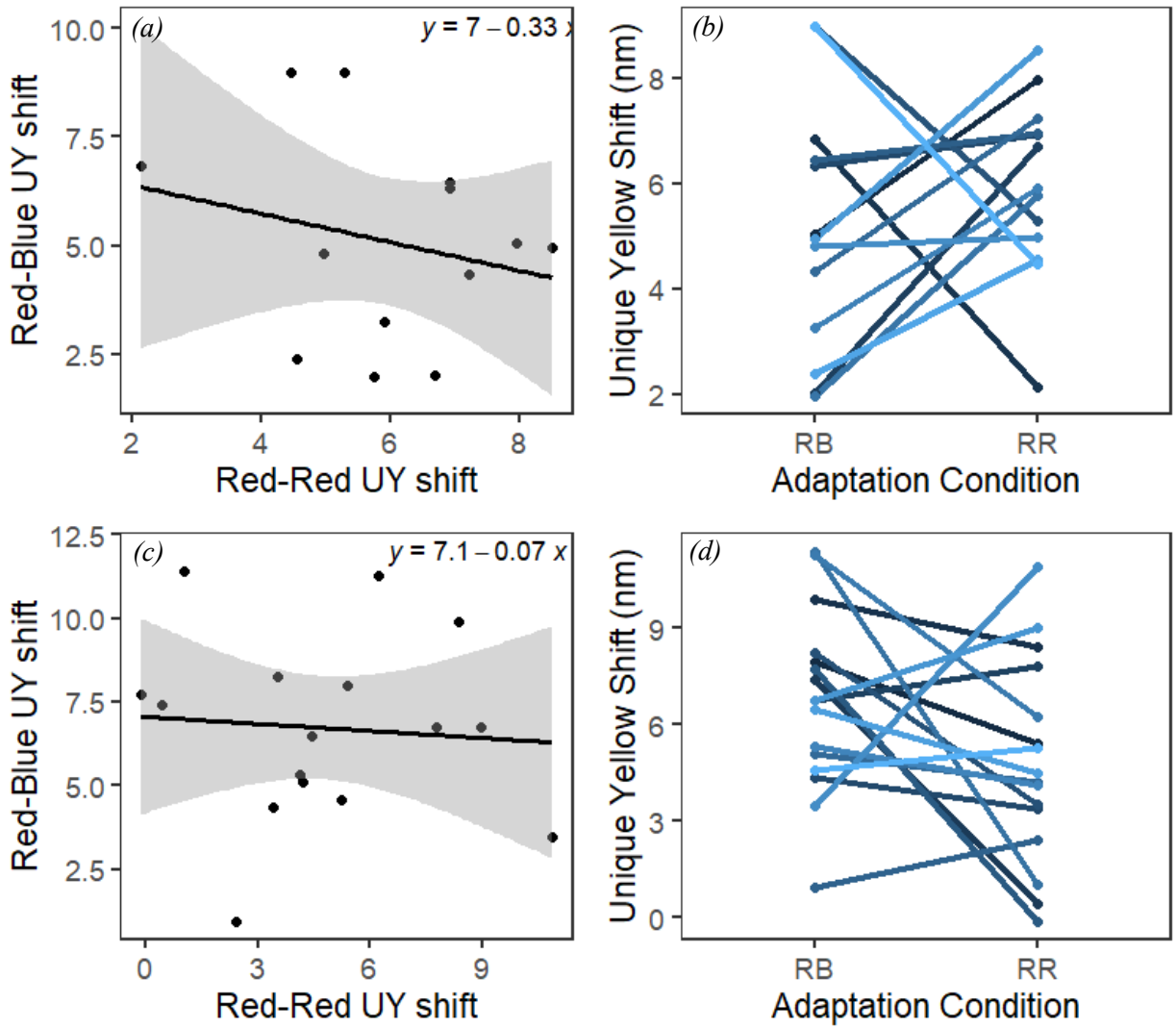


Figure 5.6 a) *Experiment 5.1: Correlations between shift in unique yellow in the right eye for the red-red condition, or the red eye in the red-blue condition. Line represents a linear trendline.* ***b)*** *Experiment 5.1: Individual participants' unique yellow shifts in the right eye for the red-red condition, or the red eye in the red-blue condition. Line represents a linear trendline.* ***c)*** *Experiment 5.2: Correlations between shift in unique yellow in non-dominant eye after red-red, or red-blue adaptation.* ***d)*** *Experiment 5.2: Individual participants' unique yellow shifts in the non-dominant eye after red-red or red-blue adaptation.:*

To analyse whether there were any trends within different participant groups, a linear mixed effect classifier was run on the data. However, this categorised the data as a single group (Figure 5.7), suggesting that there are no distinct sub-groups in the way participants adapt to the red-red and red-blue conditions that can be inferred from these data.

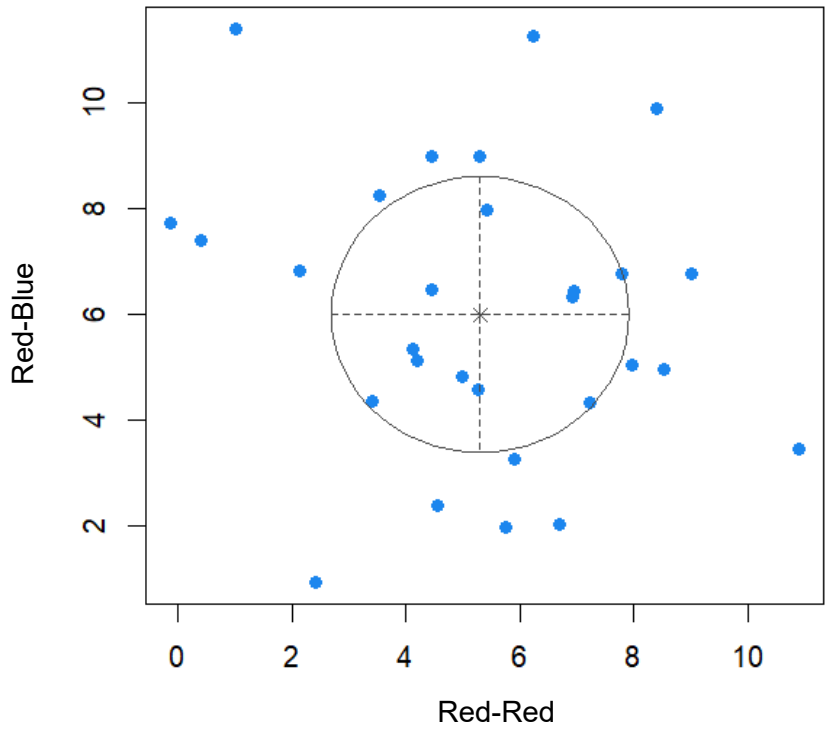


Figure 5.7: *Plot of mixed effect classifier grouping; the mixed effect classifier identifies only one group in the data. Each point represents the unique yellow shift of an individual participant in the red-red adaptation condition versus the red-blue adaptation condition, in the red-adapted eye.*

It is surprising that the strength of adaptation in the red-red versus red-blue conditions would not be well-correlated, as the previous experiments have shown strong consistency within a single participant for the strength of adaptation shown between different conditions.

5.4 General Discussion

The experiments in this chapter aimed to investigate whether adapting to one chromatic environment in one eye influenced the adaptation of the other eye when adapting to a different chromatic environment. The results of these experiments suggest that there is no significant difference in changes in the perception of unique yellow when adapting binocularly versus dichoptically to red or blue. This suggests that 60 minutes of adaptation to a coloured filter is best explained by a monocular model, and is potentially therefore occurring at a pre-cortical stage of the visual system (see Figure 5.1).

One interpretation of the lack of any interocular transfer of adaptation effects could be that this medium-term adaptation is not occurring cortically, but at an earlier stage of the visual system. Sakata and Shikamura (2022) suggest that this adaptation must be happening post-receptorally, as it does transfer between the fovea and the periphery of the retina. The adaptation in the visual system may therefore be occurring in opponent pathways, in retinal ganglion cells or the lateral geniculate nucleus (LGN). Retinal ganglion cells (RGCs) are known to show significant adaptation, however, this is generally considered to be rapid, being complete within 100ms (Brown & Masland, 2001). RGCs are considered to encode rapid departures from the mean luminance within a scene in order to establish constancy across viewing natural scenes. This suggests they may not be the best candidates for longer-term adaptation to the mean chromaticity of a scene.

A controversial suggestion is that chromatic adaptation may be taking place in the LGN. Early physiological recordings in cats suggested that the LGN does not adapt to contrast (Ohzawa et al., 1982). Later paradigms in macaques found evidence that magnocellular (M) cells in the LGN adapted to achromatic contrast, but found no evidence that parvocellular (P) cells adapted, which would be expected if there were adaptation to colour in the LGN (Solomon et al., 2004). Later, more recent fMRI data in humans has suggested that cells in the LGN do adapt to chromatic contrast. Chang, Hess, and Mullen (Chang et al., 2016) recorded BOLD signals in the LGN to achromatic or red-green stimuli either with or without 12 seconds of adaptation to red-green contrast. They found that the signal for the red-green stimulus, but not the achromatic stimulus, was reduced after adaptation, suggesting that P cells in the LGN were adapting to colour. Little is known about the time course of LGN adaptation, however, there is some data that suggests that adapting to achromatic contrast for 10-30 minutes can cause a large depression in firing rates of LGN neurons that slowly recovers over the course of an hour (Stoelzel et al., 2015), suggesting that the temporal properties of LGN adaptation may be consistent with the type of chromatic adaptation observed after longer-term adaptation to different chromatic environments. This evidence opens up the possibility of the LGN being a site of medium-term chromatic adaptation, instead of being restricted to the ideas that chromatic adaptation must either be retinal or cortical. Only recently has

evidence begun to emerge to suggest that the LGN may be involved in far more complex visual processing than was previously assumed, and medium or even long term colour adaptation may be one of its functions.

Although the pattern of results across multiple experiments presented in this thesis indicates no evidence for adaptation occurring at a cortical level, this still cannot be fully excluded as a possibility. As mentioned in the introduction, there is ambiguity as to whether long-term colour adaptation effects are able to transfer interocularly. Although there are colour-sensitive cells with binocular receptive fields, and even evidence of interocular transfer in monocular cortical cells, the psychophysical evidence consistently suggests that colour aftereffects do not transfer from one eye to the other. The only chromatic adaptation that has been consistently found to transfer between the eyes is certain versions of the McCullough effect (e.g. Mackay & Mackay, 1975; Sheth & Shimojo, 2008; White et al., 1978). It is suggested that this is able to transfer on account of the spatial component of the stimulus. Furthermore, Baker & Meese (2012) show that the extent of interocular transfer of adaptation to orientation and spatial frequency is weaker when the adapting stimulus had a low spatial frequency, and was essentially absent at very low spatial frequencies. The authors suggest that this could indicate that monocular adaptation determines the adaptive state of each eye, regardless of whether adaptation also occurs binocularly. Adaptation is prevented from transferring interocularly by the adaptive state of the monocular pathway. This could therefore explain a lack of interocular transfer for the dichoptic colour adaptation both if it is occurring at a cortical level or a pre-cortical level, as it has no spatial component.

One constant source of variability across these experiments has been the role of the individual. Individuals show a large variation in their shifts in unique yellow even under identical adaptation conditions. In this study, there was also large variation in whether participants adapted more, less, or the same amount in the dichoptic condition compared to the binocular condition. This pattern appeared random and could not be separated into clear sub-groups. It has been previously shown that neither age nor the ratio of L:M cells in the retina can account for differences in unique yellow settings (Neitz, 2002). There appears to be a factor not yet elucidated

that has a large impact on an individual's chromatic adaptation; finding this factor would probably advance our understanding of adaptation considerably.

These experiments into medium term dichoptic chromatic adaptation suggest that there is no interocular transfer of chromatic adaptation between the eyes. This can be interpreted as implying that adaptation occurs at a pre-cortical locus, however, some literature suggests that a lack of interocular transfer would be predicted regardless of whether adaptation is occurring both at monocular and binocular sites, or solely at monocular sites. There is a need for a novel paradigm for measuring whether adaptation may be occurring at a cortical level that is not susceptible to being 'blocked' by earlier stages of the visual system. However, this evidence does support the conclusion that adaptation must be happening on *at least* a monocular level, and that this is what primarily affects visual perception.

Chapter 6: Binocular Combination of Colour in the Visual Cortex

Binocular combination of colour is thought to occur in V1, with later visual areas receiving chromatic inputs that have already been combined between both eyes. However, some evidence from the neural organisation of V1, with colour-sensitive neurons being found in the centre of ocular dominance columns, as well as psychophysical observations on stereopsis, suggests that colour may be processed monocularly in V1. In this study, participants viewed LM cone or S cone isolating flickering discs either monocularly or binocularly in an fMRI scanner. The results show that BOLD activity was lower in the monocular condition compared to the binocular condition in ventral stream areas V1, V4, VO1, and VO2. We discuss different explanations for this observation, discussing the possibility of monocular chromatic representations at later stages of the visual system, and the more likely explanation of non-linear propagation of differences caused by monocular signals in V1.

6.1 Introduction

Humans have two eyes, each of which receives a slightly different visual input due to differences in viewing angle. They also receive a slightly different chromatic input due to slight differences in the cone mosaic between the eyes, differences in lens yellowing, or differences in macular pigment. In order to represent the visual environment accurately, the information falling on the retina of each eye must be combined between the eyes. The traditional view is that binocular combination occurs first in V1, due to the presence of binocularly responsive cells, and that subsequent visual areas therefore receive inputs that have already been combined between the eyes (e.g. Parker & Cumming, 2001; Mitchell et al., 2022). However, the argument has long been made that colour perception may be the exception to this rule.

The ‘textbook’ model of colour integration in V1 is influenced by the experiments of Livingstone and Hubel (Livingstone & Hubel, 1984, 1988). These showed that

double-opponent colour-selective cells are organised in V1 within cytochrome oxidase “blobs”, which themselves are found in the centre of ocular dominance columns, which are areas where neurons are grouped based on eye preference. The blobs then feed into the thin-stripe layers of V2, in which neurons show similar properties as V1 blob neurons, being either selective for red-green, yellow-blue, or broad-band stimuli, and being insensitive to orientation. The localisation of blobs in the centre of ocular dominance columns led to the belief that colour cells in the early visual cortex were monocular (i.e., only have receptive fields in one eye). This viewpoint was supported by psychophysical evidence for poor stereopsis when stimuli are isoluminant, as this suggested that colour could not be combined between the eyes to create an impression of 3D depth (Coltheart, 1973).

Later work contradicted these findings, suggesting that many colour-selective neurons in V1 are binocular, with receptive fields covering both eyes. Landisman and T’so (Landisman & Ts’O, 2002) located clusters of colour-selective neurons in macaque V1. They showed that while there was overlap between these colour-sensitive areas and blobs, the clusters tended to be larger than a single blob in size, often crossing multiple blobs and multiple ocular dominance columns. Fifty-six percent of colour-sensitive clusters crossed multiple ocular dominance columns, and 23 percent crossed ocular dominance columns that had different eye preferences. However, the most recent research again puts a caveat on this, suggesting that colour-sensitive neurons are in fact organised into “micro-maps” of cone preference which lie at the centre of blobs. Inter-blobs respond to spatially structured chromatic information, and so also receive inputs from opponent chromatic channels, however, the spatially-insensitive colour maps which are thought to underlie chromatic vision are indeed organised within individual ocular dominance columns, which may imply spatially uniform chromatic vision is monocular (Chatterjee et al., 2021).

Peirce et al. (Peirce et al., 2008) provided compelling evidence that many colour-selective neurons were driven by stimuli in both eyes. Using single unit recordings in macaque V1 and V2, they compared the responses of cells that responded to chromatic stimuli (in the form of either sinusoidal gratings or spatially uniform fields) with those that responded to achromatic stimuli. They found that very similar proportions of chromatic and achromatic neurons responded to stimuli from both

eyes (59% for colour-sensitive neurons and 55% for achromatic neurons). They also found that the colour preferences of the binocular neurons were well-matched between the eyes, giving a physiological correlate for neural combination of colour. However, even the binocular colour-sensitive neurons found in this study showed strong eye preference, with a greater response when presented with stimuli in the dominant eye. It is unclear whether the signal from the dominant eye would suppress the signal from the non-dominant eye within the neuron if stimuli were presented concurrently to each eye. It is also unclear how well this animal model translates to humans. However, later psychophysical and electroencephalography (EEG) evidence in humans has also provided support for binocular colour pathways. For example, the percepts induced by interocular switch rivalry of coloured discs in each eye give evidence for binocular competition in colour-sensitive neurons (Zhang et al., 2021), and the existence of intermodulations between spatial frequencies presented to each eye also suggests there are binocular interactions between colour percepts in visual cortex (Carter et al., 2025). There now seems little doubt that there is binocular interaction in cortical colour processing, although the dynamics of binocular colour fusion versus suppression and rivalry are still unclear (Lv et al., 2025). Overall, the evidence seems to support the idea that colour is primarily processed binocularly in V1, though there are likely also some colour-sensitive neurons that are monocular or which have a strong eye preference at the centre of ocular dominance columns.

The binocular combination of colour in later visual areas has been less investigated, partially due to the assumption that later visual areas must only process inputs binocularly, due to their functional organisation. Nonetheless, ocular dominance columns in V1 project to the thin stripes of V2, and so monocular colour signals may be maintained in V2. Using high-resolution fMRI, Nasr *et al.* (Nasr et al., 2016) showed that colour-selective stripes in V2 and V3 differed from disparity-selective stripes (which must necessarily be binocular), suggesting a potential organisational distinction between spatial and chromatic layers. Binocular neurons encoding spatial information and monocular neurons encoding chromatic information could therefore still form distinct populations in V2 and V3. However, in areas beyond V2 and V3, there is a general assumption of binocularity. Cells in V4 are sensitive to binocular disparity (Umeda et al., 2007; Watanabe et al., 2002), and are not organised into

stripes or columns corresponding to ocular dominance, although there is still a distinct separation of colour and orientation information in V4 (Tanigawa et al., 2010b). However, as tasks requiring combination of stereo information can still be performed even after selective lesioning of magnocellular layers of the LGN, the separation of colour information cannot be taken as evidence of a separation of monocular and binocular processing (Schiller et al., 1991). Although no work has directly targeted VO1 and VO2, the processing of stereo information by ventral stream regions and the lack of evidence for monocular neurons outside of V1 and V2 has also led to the assumption of binocularity in these regions. We would therefore predict that in colour-selective areas, there is a gradual reduction in the level of monocular processing, from around 40% in V1 (based off the proportions of binocular colour-sensitive neurons found by Peirce et al.), to a smaller proportion in V2 and V3, to nothing in V4, VO1, or VO2.

Another consideration is how binocular combination may vary for different chromatic stimuli. Different cone types have different trajectories to parts of the visual cortex and project to different layers within the visual cortex. For example, parvocellular cells project to different layers of V1 to koniocellular cells (Chatterjee & Callaway, 2003), and there is some evidence for S-cone pathways that bypass early visual areas and project directly to V5/MT (Seidemann et al., 1999; Sincich et al., 2004b). As a result of these different pathways, binocular combination may occur in different areas depending on the spectral properties of the stimulus. Carter et al. (2025) show some evidence for weaker binocular interactions for S-cone inputs compared to LM-cone inputs when measuring steady state visual evoked potentials (SSVEPs). In addition, S-cone inputs may be used in non-colour tasks, such as motion discrimination, leading to markedly different patterns of activity to L and M cone input (Conway, 2014).

How can we identify whether neural responses to colour are monocular or binocular using fMRI? Perceptually, the world does not appear brighter when viewed with two eyes compared to one, suggesting that binocular ‘two-input’ neurons modulate their responses when receiving input from both eyes, likely through interocular suppression. This implies that a purely ‘two-input’ neural population would not show greater activity during binocular viewing compared to monocular viewing. In contrast,

if binocular viewing elicits a stronger neural response than monocular viewing, this suggests the presence of distinct monocular 'one-input' neural populations (one for each eye) contributing additively to the response (however, note that it is difficult to distinguish whether 'one-input' neurons are truly monocular, or simply representing information from one eye due to ocular dominance or interocular suppression. As such, these neurons will be referred to as 'one-input' rather than monocular). In theory, a completely 'one-input' system would produce double the activity for binocular viewing compared to monocular viewing, while a completely 'two-input' system would show no difference between monocular and binocular viewing (this is illustrated in Figure 6.1). If both 'one-input' and 'two-input' neurons are present, the binocular response would fall somewhere in between 1-2x the monocular response.

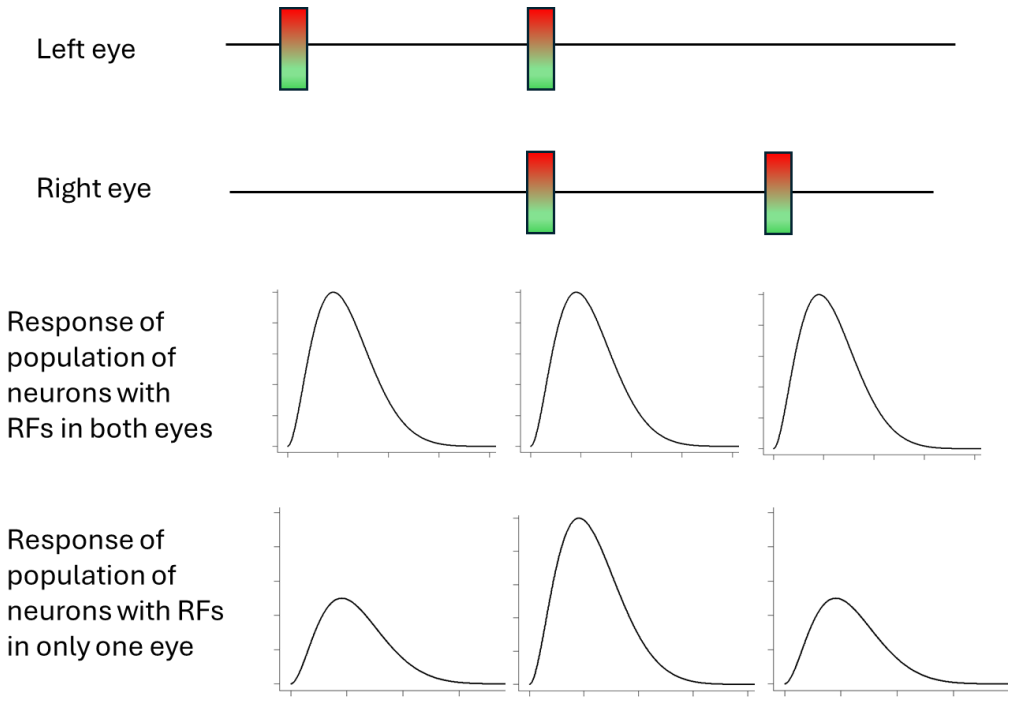


Figure 6.1: *Predicted haemodynamic response functions for populations of neurons viewing stimuli monocularly or binocularly in a condition where those neurons had 'two-input' receptive fields versus 'one-input' receptive fields.*

In this study, participants viewed S-cone or L/M-cone targeted stimuli presented either binocularly or monocularly, using a multi-primary LED system, which allowed different cone types to be silenced using silent substitution. Brain responses to the binocular presentation versus the monocular presentation of the stimuli were recorded using fMRI, and analysed across the whole brain, as well as in areas V1,

V2, V3, V4, VO1, and VO2. We aimed to identify areas in which the response to the binocular stimuli was greater than the response for monocular stimuli for either LM or S cones, and to quantify the extent to which this response was greater. We predicted that the greatest difference in response to binocular versus monocular viewing would be in V1, with a smaller difference in V2 and V3, and no difference in V4, VO1, or VO2.

6.2 Methods

Participants

Nineteen participants were tested (9 male, 10 female), aged 18-55. All participants had normal or corrected to normal (using contact lenses) vision, and normal trichromatic colour vision. Ethical approval was obtained from the Research Governance Committee at York Neuroimaging Centre on 10th March 2023. All participants provided their informed consent.

Stimuli

Stimuli were 2Hz flickering discs of magenta-cyan or purple-lime colour presented to each eye independently, with a diameter around 30º of visual angle. These colours were chosen to target cone-opponent mechanisms, and can be very roughly considered to correspond to the canonical ‘red–green’ and ‘blue–yellow’ opponent dimensions (despite being implemented here using magenta-cyan and purple-lime axes). A foveal mask of 7º diameter, made of a small piece of circular blackout material, obscured central vision, in order to take only measurements from the periphery where LM cones and S cones are both present. The discs presented to each eye were fused into a single percept by all participants. Stimuli were presented via STLAB light engines with 10 independent LED channels (SpectraTuneLAB: LEDMOTIVE Technologies, LLC, Barcelona, Spain) attached to a modified VR headset via liquid light guides (for details on the apparatus used to present the stimuli, see the Methods chapter). These were calibrated using Stockman and Sharpe’s 10-degree cone fundamentals (Stockman & Sharpe, 2000).

Stimuli were created in python using Pysilsub (Martin, 2023). See Appendix 2 for full code used for stimuli creation (Appendix 2: Code used to create LM/S stimuli in Chapter 6). STLAB video files were created for each participant at the start of each scanning session, based on their age and isoluminance values. These consisted of sinusoidal contrast modulations along the L-M or S-cone pathway presented against the same background spectrum. In the L-M condition, participants experienced an isoluminant chromatic modulation between magenta (+L-M) and cyan (-L+M). In the S-cone condition, participants experienced an isoluminant chromatic modulation between purple (+S-(L+M)) and lime (-S+(L+M)). Peak cone contrasts were 9% for LM cones and 40% for S cones. These values were chosen based on prior work, with the aim of producing broadly comparable response magnitudes in early visual cortex rather than performing an explicit contrast-matching procedure.

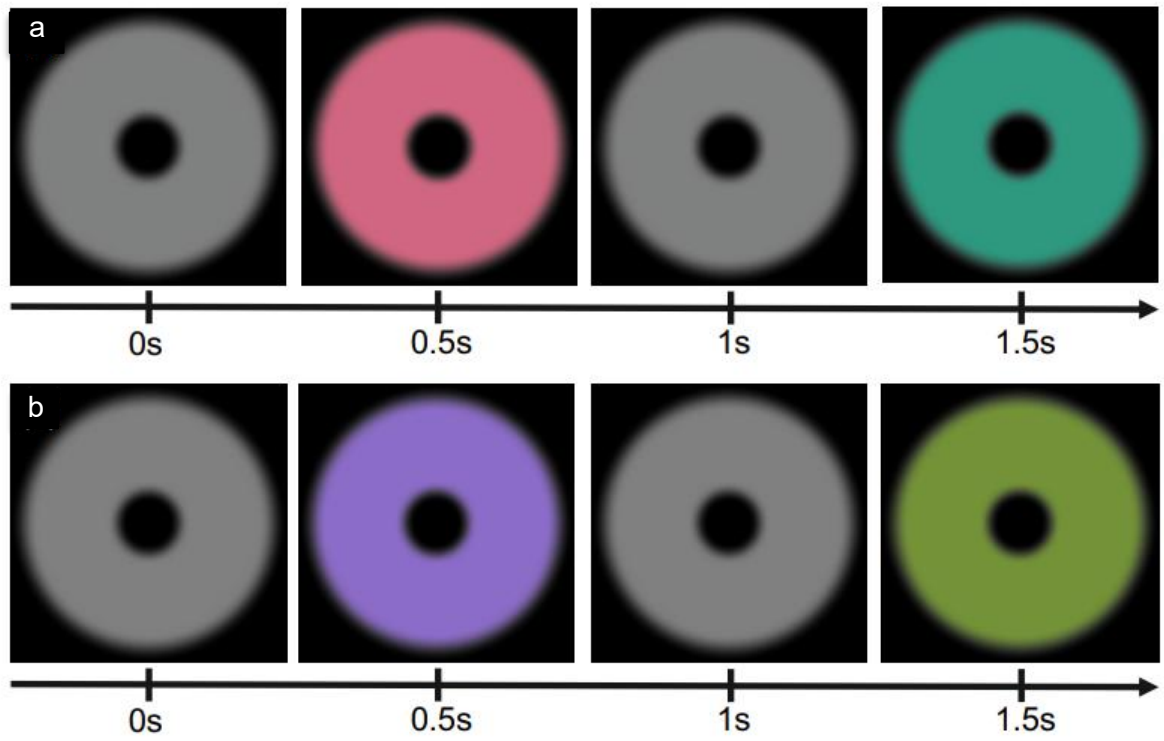


Figure 6.2: a) *One cycle of flicker for a stimulus from the L-M condition. The stimulus flickers between magenta, cyan, and the background neutral grey.* ***b)*** *One cycle of flicker for a stimulus for the S condition. The stimulus flickers between purple, lime, and the background neutral grey. From: Segala, 2023.*

In order to ensure that stimuli were isoluminant for participants, a minimal flicker calibration task was performed on an Iiyama VisionMasterTM Pro 510 display (800 x 600 pixels, 60 Hz refresh rate) for each participant before scanning, and their LM and S cone isoluminance values were used to create unique stimuli for each participant (procedure based on Baker et al., 2024). This task involved participants viewing a disc flickering at 2Hz within either the L-M cone space (between magenta and cyan) or within S-(L+M) cone space (between purple and lime). Participants adjusted the angle in cone space across 10 trials per cone condition until the flicker of the stimulus appeared to be as close to invisible as possible. An example of one cycle of this task is shown in Figure 6.2. The resulting L-M and S cone angles were used to modify stimulus contrasts during stimulus presentation. The L-M and S-(L+M) stimuli were therefore defined by cone contrast, with contrasts being modulated by the L-M and S-(L+M) isoluminance values, as well as a correction for age using the CIE 2006 Physiological Observer, in order to account for the effect of lens yellowing (see PySilSub, (J. T. Martin et al., 2023)).

The background spectrum was determined by setting all channels on the first light device (STLAB 1) to half maximum output, then finding the equivalent settings on the second device (STLAB 2). This gave a grey background with an approximate luminance of 68.5 cd/m².

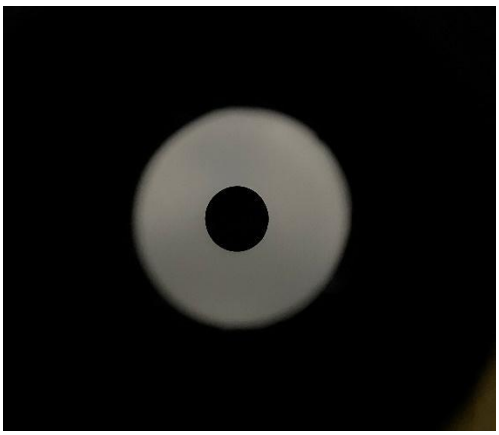


Figure 6.3: *Photograph of background stimulus presented to participants in one eye.*

6.2.1 Experimental Design

An event-related fMRI design was used, consisting of 4 runs of 42 trials. Eight conditions were presented 6 times per run, with these conditions consisting of LM left eye, LM right eye, S left eye, S right eye, 2x binocular LM, 2x binocular S. The binocular conditions were duplicated to ensure there were an equal number of events due to there being separate left and right eye trials in the monocular condition. This design therefore compressed into four conditions presented 12 times per run: monocular LM, monocular S, binocular LM, binocular S. LM trials appeared to participants to flicker between magenta and cyan, and S trials appeared to flicker between purple and lime. On monocular trials, the non-stimulated eye viewed the neutral background illumination.

Stimuli were presented in alternate 30 second ‘blocks’ of L-M and S cone conditions, in which each of the 8 conditions were presented in a random order. Each trial lasted 3 seconds with an inter-trial interval of at least 3 seconds, and with at least 2 seconds of buffer at the start and end of each block.

Attentional probes were randomly presented throughout the scan, which consisted of a 50% dimming of the background. These were presented 24 times per run, and were acknowledged by participants with a button press, in order to help participants to continue attending to the stimuli.

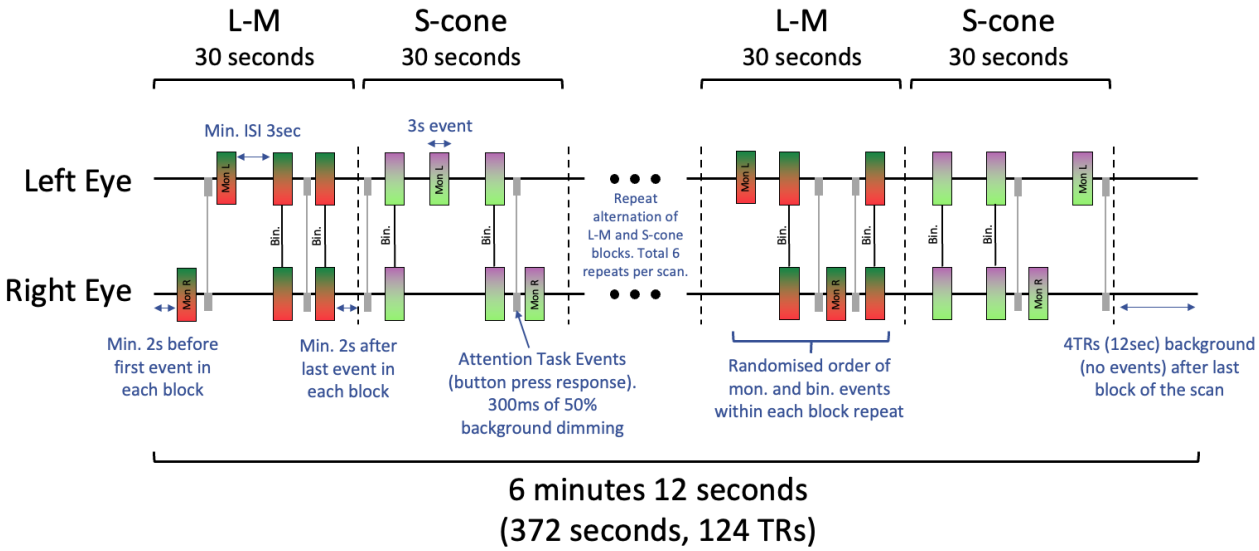


Figure 6.4: *Schematic of experimental design used. Credit: Lauren Welbourne, 2023.*

6.2.2. MRI Data Acquisition

Images were acquired on a 3T Siemens Magnetom Prisma MRI scanner and a Siemens 64-channel head and neck coil. High resolution T1-weighted (TR 2.4s; TE 2.28ms; voxel size 0.8 x 0.8 x 0.8 mm; 8° flip angle; FOV 256 x 256 x 256 mm) structural scans were acquired using a generalized auto-calibrating partially parallel acquisition (GRAPPA) with a multi-band acceleration factor of 2.

Functional images depicting blood-oxygen level dependent (BOLD) levels were acquired with a T2*-sensitive gradient-recalled echo pulse sequence (TR 3s; TE 36.6ms; voxel size 2.3 x 2.3 x 2.0 mm; 75° flip-angle; FOV 280 x 280 mm; 72 slices). Slices were acquired using an interleaved method and a multiband acceleration factor of 2. Each functional scan lasted just over 6 minutes and yielded 124 volumes, with a total of four functional scans being recorded for each participant.

6.2.3. Structural Data Preprocessing

Reconstructions of each participant's brain were created using their T1-weighted images. Freesurfer v6.0 (https://surfer.nmr.mgh.harvard.edu/) recon-all, which performs the freesurfer cortical reconstruction process, was used to construct the

images and the Brain Extraction Tool from FSL (FMRIB Software Library) v6.0 (Smith, 2002) was used to skull-strip the images.

6.2.4. Functional Data Preprocessing

Data preprocessing was performed for each of the four functional runs using FSL (version 6.0, FSL, https://fsl. fmrib.ox.ac.uk/fsl/: Jenkinson et al., 2012) and custom python scripts. Motion correction (MCFLIRT (Motion Correction FMRIB Linear Image Registration Tool); Jenkinson et al., 2002), brain extraction (BET; Smith, 2002), spatial smoothing with a Gaussian kernel (FWHM = 5mm), slice timing correction (using custom slice timing correction), and high-pass temporal filtering (cut-off = 100s) were applied using FEAT. Functional runs were registered to each participant's T1-weighted structural scan using FLIRT (FMRIB's Linear Image Registration Tool, Jenkinson and Smith, 2001), and combined across the four functional runs using FEAT (FMRIB Expert Analysis Tool, Jenkinson et al., 2012). For the whole brain analysis, the data was also registered MNI space using FNIRT (FMRIB Nonlinear Image Registration Tool, Andersson et al., 2008) and combined across the four functional runs using FEAT.

6.2.5. Statistical Analysis

Statistical analysis was conducted using FEAT and R. Four regressors were investigated: LM monocular, S monocular, LM binocular, and S binocular. These regressors were constructed by convolving the stimulus presentation timings with a canonical double gamma haemodynamic response function (HRF) waveform. The resulting general linear model was applied at each voxel to identify significant BOLD responses.

A region of interest analysis was conducted using FEATQUERY for six regions of interest (V1, V2, V3, V4, VO1, VO2), which were selected due to their position on the ventral stream and known involvement in colour processing. Voxels were selected for each participant based on ROI masks constructed using Freesurfer v6.0 and the

Benson brain atlas (Benson et al., 2014), which allowed for the ROI masks to be restricted based on eccentricity to only include voxels corresponding to between 3.5- and 15-degrees radius. The functional data were aligned to the same individual structural space as the ROI masks. The FEATQUERY output gave mean beta changes for each ROI for each regressor which were then statistically analysed using R for the contrasts binocular > monocular for each colour condition.

An exploratory whole brain analysis was conducted using FEAT in order to identify any further areas where binocular activity was greater than monocular activity. Participants' functional data were transformed to MNI (Montreal Neurological Institute) space, in order to transform all functional data onto a common brain, and combined across participants using a second level mixed-effects analysis in FLAME (FMRIB Local Analysis of Mixed Effects, (Smith et al., 2004)) for six contrasts: monocular LM, monocular S, binocular LM, binocular S, binocular LM – monocular LM and S binocular – LM monocular.

6.3 Results

6.3.2. ROI

Six regions of interest (V1, V2, V3, V4, VO1, and VO2) were investigated to compare mean beta responses during monocular or binocular presentation of LM or S cone isolating stimuli. Figure 6.5 shows that for areas V1, V4, VO1, and VO2, responses were greater in the binocular condition compared to the monocular condition for both LM and S cone stimuli. The increase in activity in the binocular condition compared to the monocular condition is greatest in later visual areas VO1 and VO2).

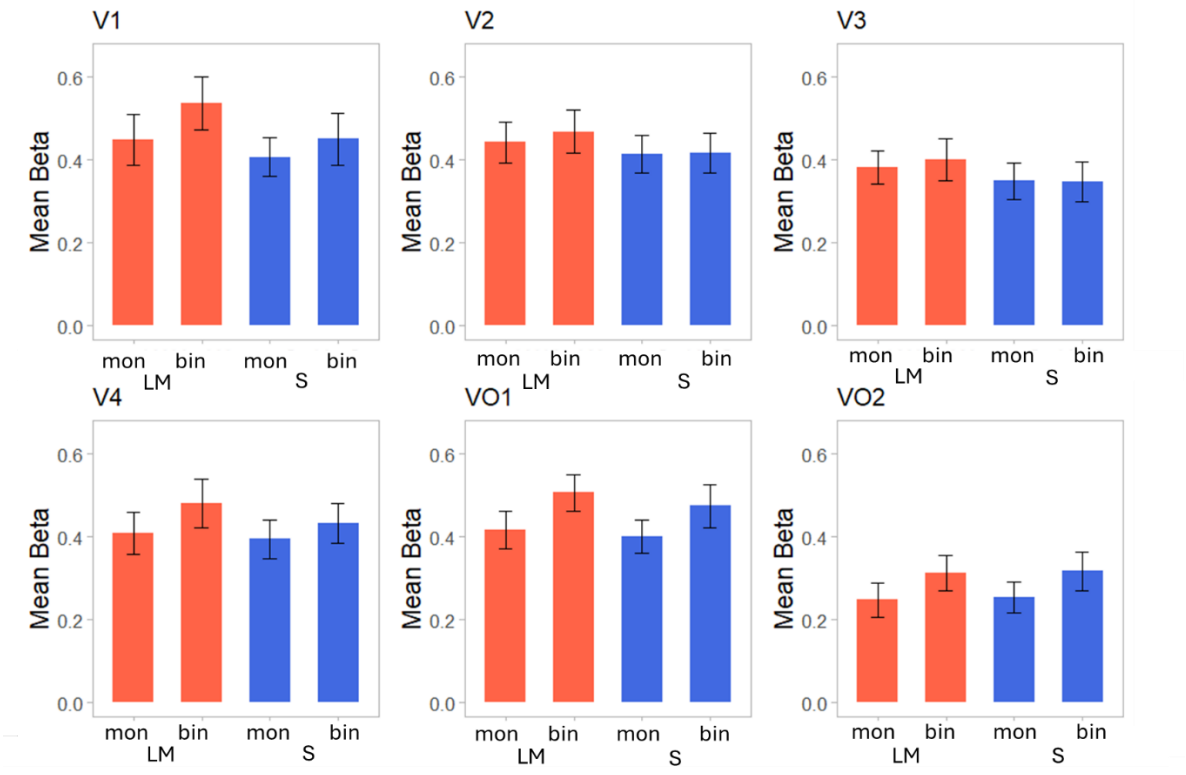


Figure 6.5: *Mean beta values (n = 19) for monocular versus binocular stimulus presentation for LM or S cone isolating stimuli in each region of interest. Error bars represent +/- one standard error of the mean.*

In order to statistically analyse this pattern, mean beta values for each participant were entered into a three-way repeated measures ANOVA for 6 regions of interest (V1, V2, V3, V4, VO1, VO2) with factors of colour condition (LM or S) and eye condition (binocular or monocular).

The main effects of ROI and eye condition were both significant (ROI: $F(3.17,57.04) = 7.43$, $p < .001$, $\eta^2 = .29$, Binocularity: $F(1,18) = 6.69$, $p = .019$, $\eta^2 = .27$). As can be seen in Figure 6.5, the main effect of ROI is likely driven by different levels of absolute activity in the different brain areas, and the main effect of eye condition is likely driven by generally greater activity in the binocular condition compared to the monocular condition. However, there was no significant main effect of colour condition ($F(1,18) = 3.13$, $p = .094$), suggesting that there was no significant overall difference between activation to LM cones or S cones.

However, there was a significant interaction between ROI and colour condition ($F(3.00, 53.93) = 6.97$, $p < .001$, $\eta^2 = .28$), which indicated that there may be

differences between activity in the LM cone condition compared to the S cone condition for some ROIs. There was also a significant interaction between ROI and eye condition ($F(2.84, 51.04) = 5.61$, $p = .003$, $\eta^2 = .24$). Figure 6.5 suggests this may be driven by greater activity in the binocular condition than the monocular condition for some ROIs. There was no significant three-way interaction between ROI, cone condition, and eye condition ($F(2.39, 42.99) = 0.71$, $p = .522$). This indicated that the amount of activity in the binocular condition compared to the monocular condition did not change for different colour conditions in different ROIs.

Based on the significant interaction between ROI and colour condition, the effect of colour condition was further examined for each ROI using paired t-tests, Bonferroni corrected for multiple comparisons. There was a significant difference between the LM and S cone conditions in V1 only (see Table 6.1 for full summary of results). This may be indicative of S-cone amplification in later visual areas.

Table 6.1: *Results of pairwise t-tests for colour condition at each ROI*

ROI	df	t	Adjusted p value
V1	37	2.48	.018*
V2	37	1.79	.082
V3	37	1.86	.071
V4	37	1.54	.132
VO1	37	1.23	.227
VO2	37	-0.34	.735

Based on the significant interaction between ROI and eye condition, the effect of eye condition was further examined for each of the six regions of interest using Bonferroni-corrected paired t-tests. Contrary to expectations, there was a significant difference between the monocular and binocular conditions in V1, V4, VO1, and VO2, but not V2 or V3 (see Table 6.2 for full summary of statistical results). These results are shown in Figure 6.6, which suggests that the significant differences are

driven by greater activity in the binocular condition compared to the monocular condition in all cases.

Table 6.2: *Results of pairwise t-tests for eye condition at each region of interest.*

ROI	df	t	Adjusted p value
V1	37	2.52	.016*
V2	37	0.61	.544
V3	37	0.35	.729
V4	37	2.69	.011*
VO1	37	3.98	< .001***
VO2	37	3.43	< .001***

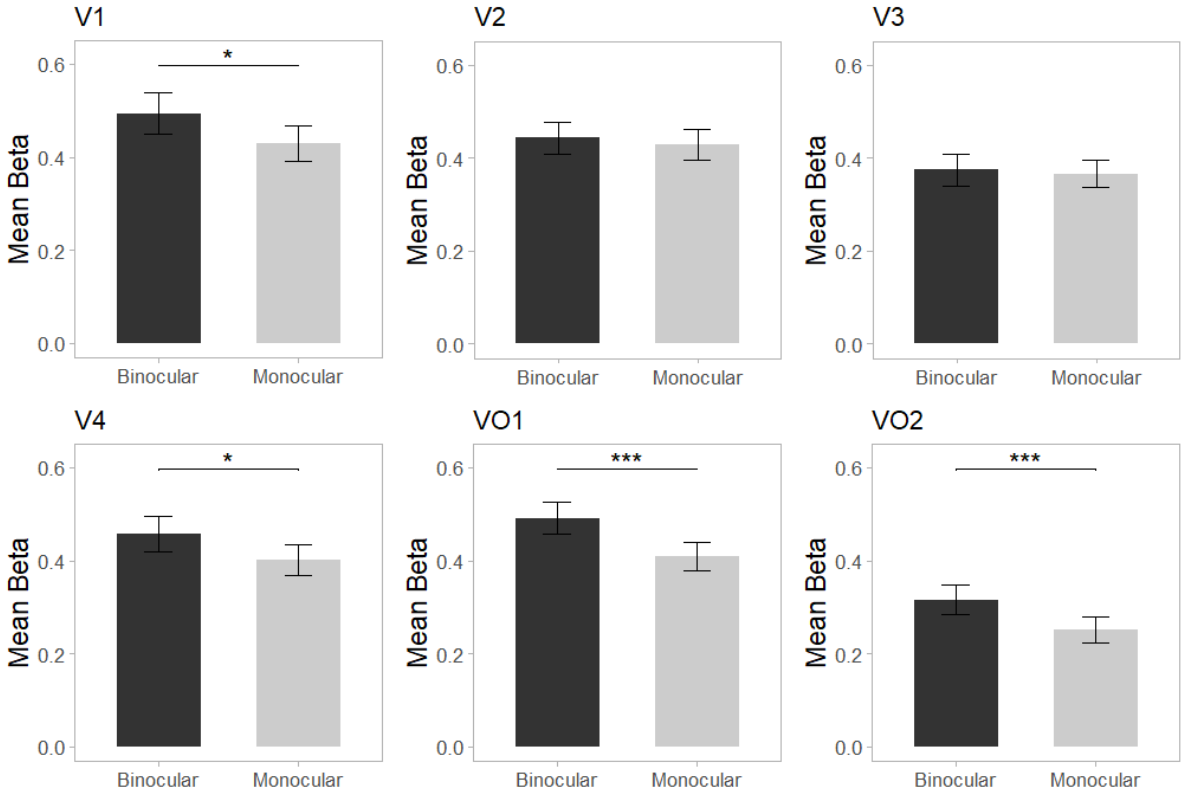


Figure 6.6: *Mean betas values (n = 19) for disc stimuli presented to each eye separately or simultaneously in V1 to VO2. Error bars indicate +/- one standard error of the mean.*

In order to quantify the binocular advantage in areas with significant binocular > monocular activity, we calculated the percentage increase in the mean beta values in the binocular condition compared to the monocular condition. These are shown in

Table 6.3. This shows that, contrary to predictions, the increased activity in the binocular condition is greater in later visual areas.

Table 6.3: *Percentage increase in mean beta signal in binocular condition compared to monocular condition.*

ROI	LM	S
V1	19.28%	10.67%
V4	17.93%	9.74%
VO1	21.62%	18.19%
VO2	26.08%	24.85%

6.3.1. Whole Brain

To identify if there were any further visual areas that had a greater response to binocular chromatic stimulation compared to monocular chromatic stimulation, we ran an exploratory whole brain analysis. The results of the FSL whole brain group analysis were plotted on Freesurfer fsaverage inflated brain surfaces using pysurfer (https://pysurfer.github.io/). Figure 6.7 shows the z-stat (an image which shows the statistical significance of activity at each voxel) cluster corrected and thresholded at 2.3 (p = .01) for monocular and binocular activation to the LM-cone stimuli. Figure 6.8 shows the z-stat cluster corrected and thresholded at 2.3 (p = .01) for monocular and binocular activation to the S-cone stimuli. As is expected, there is considerable activity in all conditions throughout visual areas, but no activity in strongly retinotopic areas of early visual cortex corresponding to the central 7 degrees of visual angle that were masked.

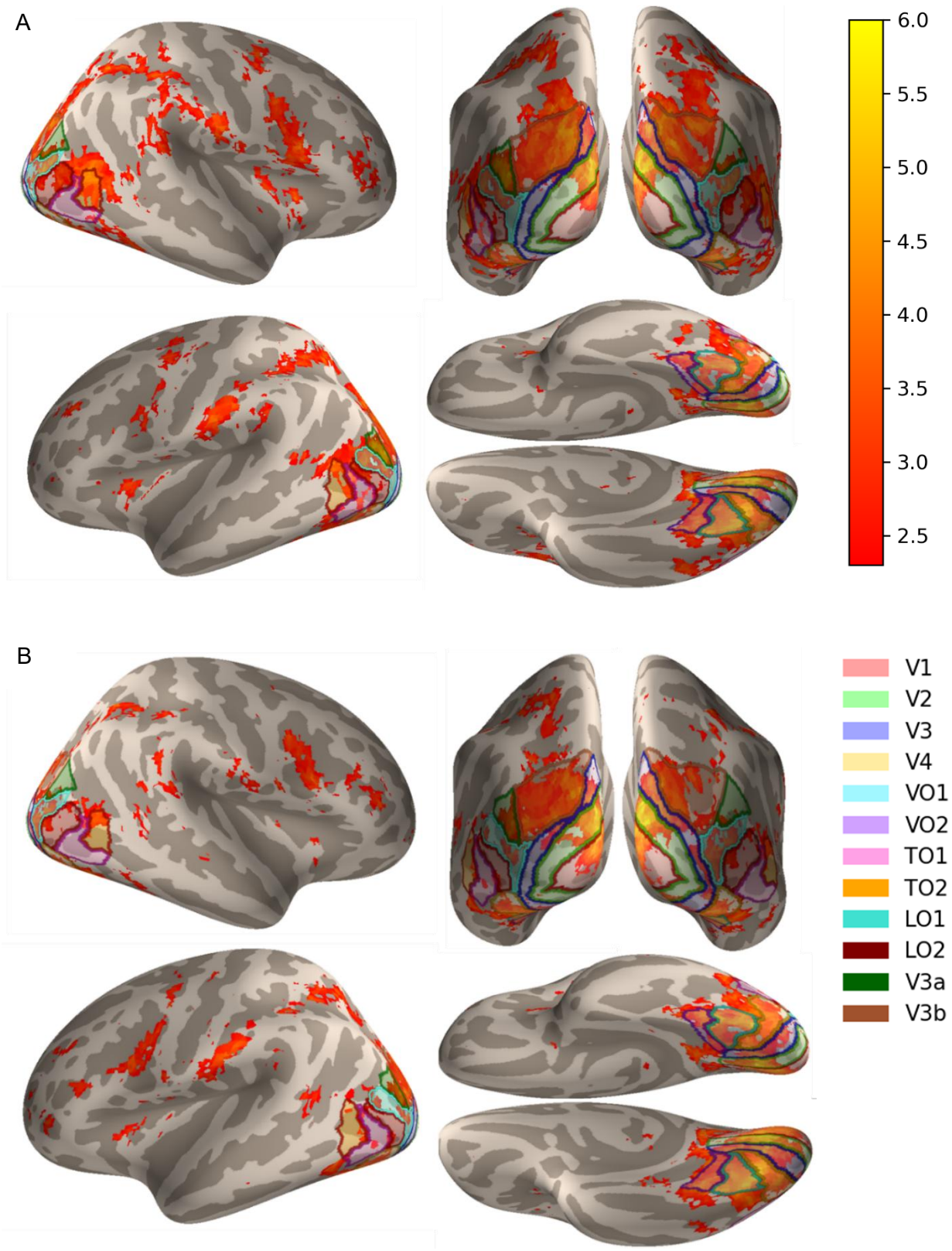


Figure 6.7: *Lateral, caudal, and ventral views A: Monocular LM activity. Cluster corrected and thresholded z-stat at 2.3. B: Binocular LM activity. Cluster corrected and thresholded z-stat at 2.3. ROIs are generated from the Benson atlas, and represent whole regions without eccentricity restriction.*

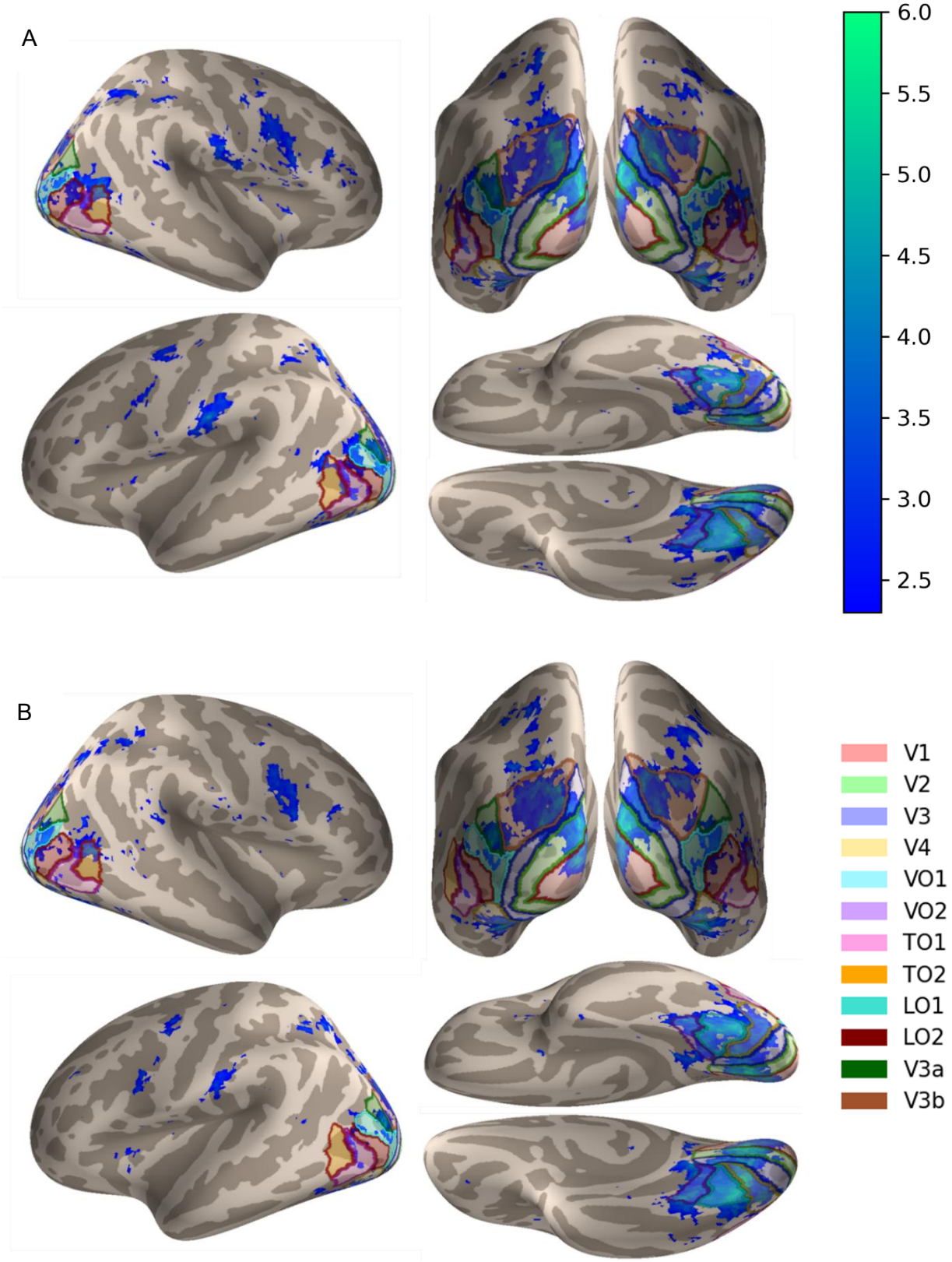


Figure 6.8: *Lateral, caudal and ventral views. A: S-cone monocular activation. Cluster corrected and thresholded (at 2.3) z-stat. B: Binocular S-cone activation. Cluster corrected and thresholded (at 2.3) z-stat. ROIs are generated from the Benson atlas, and represent whole regions without restricting for eccentricity.*

Figure 6.9 shows the cluster corrected and thresholded (at 1.96, p = .05) z-stat for the binocular LM > monocular LM contrast. The results show greater activation in the binocular condition along the ventral stream. Overlaying brain regions suggests that the majority of the binocular > monocular activity occurs along the ventral stream, in V1, V4, VO1, and VO2.

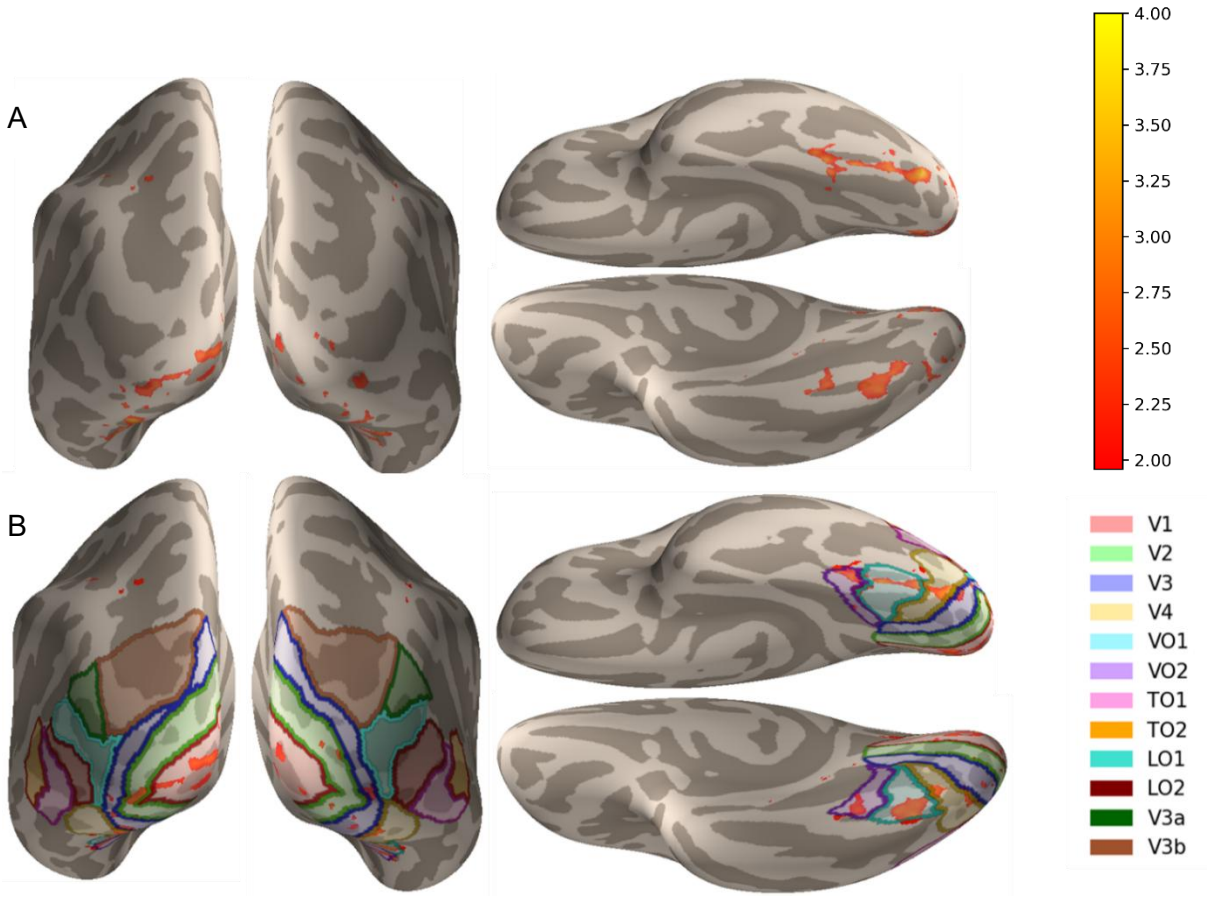


Figure 6.9: *LM-cone caudal and ventral views with thresholded and cluster-corrected z-stat at 1.96 (p < .05). A: Without ROIs overlaid, B: With ROIs overlaid. ROIs are generated from the Benson atlas, and represent whole regions without restricting for eccentricity.*

Figure 6.10 shows the thresholded z-stat (p = .05) for the binocular S > monocular S contrast. The results show some level of greater activation in the binocular condition along the ventral stream, similar to the LM condition, although less activity survives thresholding and cluster correction. Overlaying brain regions suggests that the majority of the binocular > monocular activity occurs in VO1 and VO2.

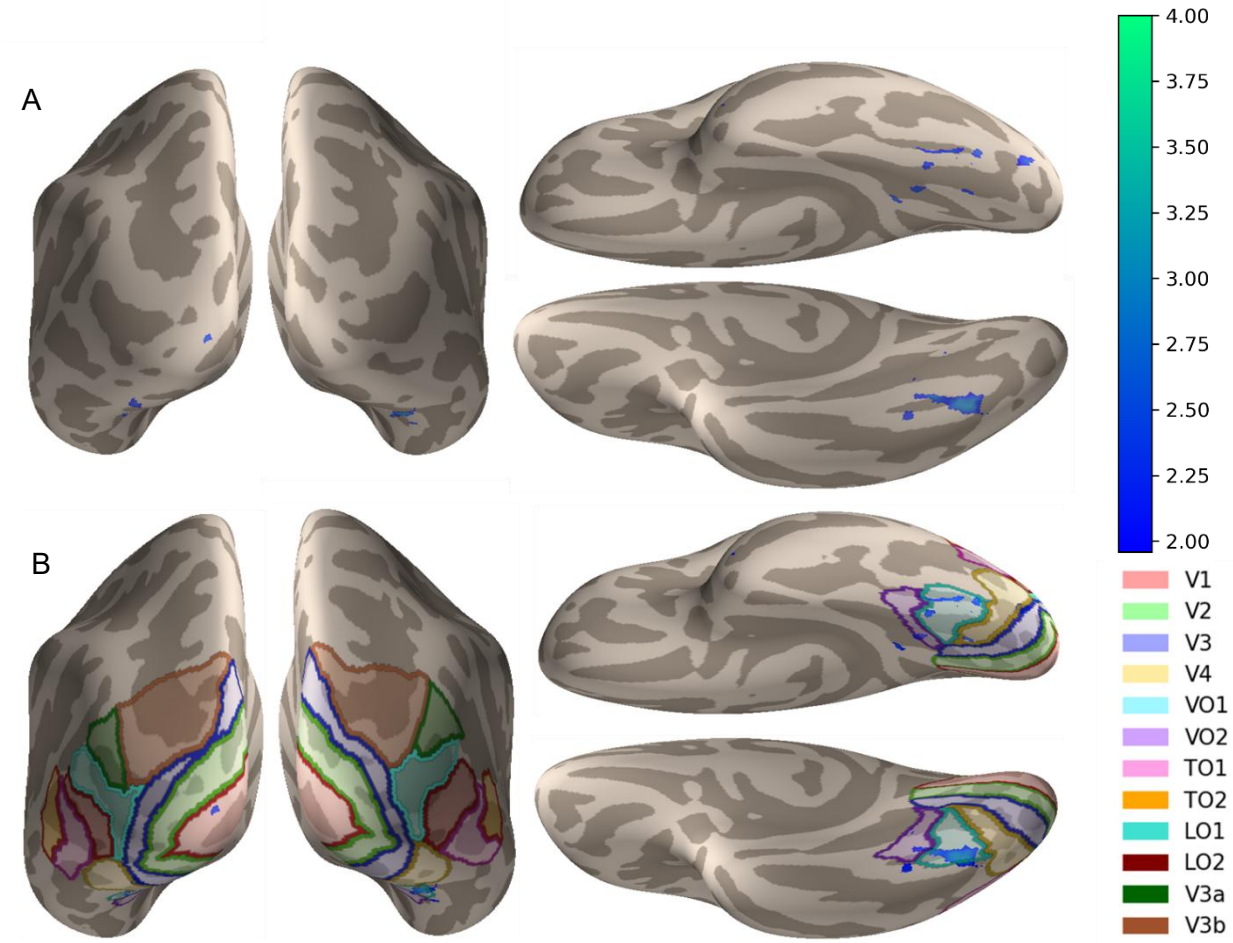


Figure 6.10: *S-cone caudal and ventral views with thresholded and cluster-corrected z-stat at p < .05. A: Without ROIs overlaid, B: With ROIs overlaid. ROIs are generated from the Benson atlas, and represent whole regions without restricting for eccentricity.*

An analysis contrasting the left and right eye, in order to account for the potential influence of the blind spot, is reported in Appendix 3. This suggests the results reported here are not due to differences caused by the blind spot in the monocular vs binocular conditions. A linear regression between the monocular and binocular signal in each participant for V1, V4, VO1, and VO2 is reported in Appendix 4. This suggests that participants show a roughly linear relationship between their monocular and binocular responses. The results of a comparable experiment examining monocular versus binocular responses to luminance is reported in Appendix 5, suggesting that the binocular > monocular effects found in regions of interest in this study are specific to colour, and do not generalise to achromatic stimuli.

6.4 Discussion

This experiment compared the brain response using fMRI to flickering discs presented either binocularly or monocularly, and targeting either LM cones or S cones, in order to identify brain regions where the response to binocular presentation was greater than the response to monocular presentation. A region of interest analysis localised the binocular > monocular activity to V1, V4, VO1, and VO2. Quantifying the magnitude of the binocular > monocular activity suggested that the size of the binocular enhancement was greater in later visual areas, contrary to predictions, with the largest difference between binocular and monocular activity seen in VO1 and VO2. The whole brain analysis confirmed that for both LM- and S-cone targeting stimuli, there was a greater response in ventral stream areas to stimuli presented to both eyes binocularly than stimuli presented monocularly. The results presented in Appendix 5 show that this binocular > monocular activity is not present in visual areas for achromatic discs, suggesting that the pattern of results found in this experiment are specific to chromatic stimuli.

The finding of binocular > monocular activity could, on a surface level, be interpreted to provide evidence for the existence of populations of neurons in the ventral stream that receive input only from one eye ('one-input' neurons; see Figure 6.1). The binocular advantage can be explained by the responses of two separate populations of neurons, each of which responds individually to stimuli presented to each eye monocularly, but both of which respond together to stimuli presented to both eyes binocularly. Although the small magnitude of the binocular advantage implies there are also populations of cells that are receptive to both eyes, this nonetheless supports the idea that some colour-sensitive neurons retain receptive fields in only one eye, even at late stages of the visual system.

However, there are alternative explanations for the results that do not necessitate 'true' monocular cells at later stages of the visual cortex. One explanation could be that some colour-sensitive neurons do have receptive fields in both eyes, but have a strong preference for one eye over the other, (such as found by Peirce et al., 2008) therefore producing responses like those of a 'true' monocular neuron. However, two-photon calcium imaging studies suggest that during binocular stimulation,

binocular neurons in V1 with strong ocular dominance preferences are suppressed, and binocular neurons with preferences for both eyes were enhanced, resulting in similar levels of activity for binocular viewing compared to monocular viewing (S.-H. Zhang et al., 2024). This suggests that binocular neurons with strong ocular dominance preferences would not produce the pattern of results we observed; if they were the underlying architecture, then we would predict responses where binocular activity is equal to monocular activity. Another alternative explanation is that there are nonlinearities before binocular summation that lead to the suppression of the weaker eye, such that only the output of the more strongly stimulated eye drives binocular neurons – a 'winner-takes-all' model (Read & Cumming, 2003). However, these nonlinearities are usually suggested to occur in near-threshold stimuli, unlike the above-threshold stimuli used in the present experiment. Furthermore, luminance flicker contrast-matching experiments for disc stimuli suggest that binocular combination for these unstructured stimuli is linear, and is not consistent with a 'winner-takes-all' model (Segala et al., 2023).

However, a simpler and more parsimonious explanation for the greater binocular > monocular difference in later visual areas compared to earlier visual areas may be linked to the progressively nonlinear response properties along the ventral visual stream. According to this explanation, a relatively small binocular > monocular difference arises initially in V1, due to monocular responses within ocular dominance columns. Responses in V1 are approximately linear, such that small differences in input produce correspondingly small differences in the BOLD signal. As visual signals are propagated to later visual areas, including V4, they are subject to increasingly nonlinear response functions. Neurons in these regions often exhibit saturating responses, such that modest differences in input can lead to disproportionately large differences in measured activity. Consequently, the small binocular > monocular difference present in V1 could be amplified as it passes through these nonlinear transformations, resulting in a larger apparent effect in V4, despite the absence of monocular neurons in later visual areas. This form of progressive nonlinearity has been well documented in the visual system (e.g., Liu & Wandell, 2005), and provides a straightforward explanation for why binocular–monocular differences might increase rather than attenuate across processing stages. In this explanation, later visual areas do not generate binocular–monocular

differences or possess monocular neurons, but instead reflect an amplified version of an earlier V1-originating signal.

Another finding from the present study was that V1 responses were stronger for LM-cone–targeting stimuli than for S-cone–targeting stimuli. This is to be expected due to the known greater representation of L and M cones compared to S cones in visual cortex (Du et al., 2022b). However, there was no significant difference between the magnitude of LM cone and S cone activity in later visual areas. This may reflect the amplification of S cone signals through the visual system. This pattern of results is consistent with previous studies which have found greater LM than S cone representation in V1, but not in later visual areas (Du et al., 2022b; Liu & Wandell, 2005).

There was no significant interaction between the colour of the stimulus and whether the stimulus was presented monocularly or binocularly, which suggests that the difference between the monocular and binocular activity was not dependent on the cone type stimulated. In other words, the evidence suggests that different colours are combined in ‘two-input’ neurons to the same degree, regardless of the cone types stimulated. This contradicts previous research which suggested that binocular interactions may vary depending on the cone type stimulated (Carter et al., 2025). However, it is notable that the direction of the effect was the same, with weaker binocular responses for S-cones (see Table 6.3), but in the present study this effect was observed but did not reach statistical significance. However, the effect does appear to be specific to colour processing, as achromatic stimuli did not produce a significant difference in activity in any area when presented monocularly versus binocularly (see Appendix 5 for the full results of a companion study comparing responses to achromatic stimuli). This is consistent with the idea of populations of monocular colour neurons within ocular dominance columns in V1 being insensitive to achromatic changes in stimulus properties.

In conclusion, this study provides evidence that differences in colour-related responses to monocular and binocular stimulation emerge early in the visual system and are expressed more strongly in later ventral visual areas, with the largest binocular > monocular BOLD responses observed in VO1 and VO2. The increase in

the magnitude of this effect across visual areas is consistent with the presence of nonlinear response properties along the ventral stream, whereby relatively small differences present in early visual cortex may be amplified at later processing stages. In addition, the absence of significant differences between cone opponent mechanisms suggests that colour information may be combined across the eyes in a similar manner across different chromatic pathways. However, this binocular > monocular effect was not found for achromatic stimuli (see Appendix 5), suggesting that this pattern of responses is unique to colour processing.

Chapter 7: Discussion

7.1 Summary of Findings

Findings of long-term shifts in colour perception following adaptation to altered colour environments suggest that the visual system is able to plastically adapt to substantial changes in the chromatic environment. However, mechanisms of long-term colour adaptation are not well-characterised. The point at which adaptation transitions from the ‘short-term’ to the ‘long-term’ is unknown, as is the ‘dose-dependence’ of adaptive mechanisms on the luminance and duration of the adapting environment. It is also unclear whether longer term chromatic adaptation occurs at a cortical or pre-cortical stage, or whether adaptation effects interact between the eyes. The combination of colour between the eyes affects the interpretation of research on interocular transfer of adaptation, and is also a topic of debate. The work covered in this thesis has therefore aimed to address the influence of adapting colour, adaptation duration, and adapting luminance on medium-term chromatic adaptation. It has also aimed to investigate the recovery process of medium-term chromatic adaptation, whether chromatic adaptation is a monocular or binocular process, and how chromatic signals are combined between the eyes in the cortex. In order to achieve this, we have used well-established psychophysical methods of investigation, using a 1934 Wright colorimeter for colour judgement tasks, as well as novel techniques involving using a multiprimary system for silent substitution in each eye individually in an fMRI scanner.

Chapter 3 investigated the influences of the duration, luminance, and colour of the adapting environment using colour-filtered goggles. Unique hues were measured on the Wright colorimeter before adaptation, 5-minutes post-adaptation, and 60-minutes post-adaptation. The results suggest that after red adaptation, unique yellow shifted to longer wavelengths, with the effect saturating between 15 and 60 minutes of adaptation; there was no significantly greater shift after 4 hours of adaptation compared to 60 minutes. After blue adaptation, unique yellow shifts were in the

opposite direction, but smaller than in the red condition, and saturated before 15 minutes of adaptation. The same pattern of results was found when measuring unique green as an alternative outcome measure. In all conditions, unique hue settings returned to pre-adaptation settings within 60 minutes post-adaptation. A second experiment investigating luminance showed that higher luminance levels significantly increased the magnitude of unique yellow and unique green shifts, showing a linear relationship. However, when modelling the predicted unique hue shifts for equiluminant red and blue filters, the observed data from Experiment 1 still deviated from predictions, indicating that luminance alone could not fully account for the differences in aftereffect magnitude between the red and blue conditions. A model of unique yellow using the L/M cone ratio predicted maximum shifts in opposite directions for red and blue adaptation, which were in the same direction as those found in the experiment, but much larger in magnitude. We suggest that the luminance and duration of the adapting environment interact to determine the extent to which this maximum shift is achieved.

Chapter 4 investigated the recovery process of medium-term colour adaptation. Experiment 1 showed that after 60 minutes of adaptation there were no significant differences in unique yellow settings between a pre-adaptation measurement point, and either 30- or 60-minutes post-adaptation. This suggests that the adaptation aftereffects decay quickly. Experiment 2 explored whether adaptation recovery depends on the presence of visual input. Participants adapted to red filters for 60 minutes, then spent the 60-minute recovery period either in normal daylight conditions or in complete darkness. There was no significant difference in unique yellow settings between the 60-post adaptation timepoints in the two conditions. In order to conclude that there was no difference between unique hue settings at the 60 minute post-adaptation timepoint in each condition, we ran Bayes factor paired t-tests. These confirmed the visual pattern that there was no difference between unique hue settings at 60-minutes post-adaptation in the two conditions. This evidence suggests that recovery occurs passively and does not require visual stimulation.

Chapter 5 aimed to investigate whether medium-term colour adaptation was occurring at a cortical locus by testing for interocular transfer effects. In Experiment

1, participants adapted for 60 minutes either binocularly (both eyes adapted to the same colour) or dichoptically (each eye adapted to a different, luminance-matched colour: red and blue). Unique hue settings were measured before and after adaptation. The results showed no significant difference in the magnitude of the unique yellow shift between the binocular and dichoptic conditions, suggesting that adaptation in one eye does not significantly affect the adaptive state of the other. Experiment 2 addressed the possibility that eye dominance might obscure interocular effects. In this experiment, participants' dominant eye was consistently adapted to blue, and measurements were taken from the non-dominant eye, which was adapted to red. This design ensured that any transfer effects would be measurable in the non-dominant eye. The results replicated those of Experiment 1, again showing no significant difference between binocular and dichoptic adaptation conditions. In order to confirm the null hypothesis, Bayes Factor paired t-tests were again conducted, which also supported the interpretation that there was no difference in unique hue settings between the eyes when adapted binocularly versus dichoptically. Together, these findings suggest that medium-term chromatic adaptation effects are monocular, potentially indicating that they arise at a pre-cortical stage of visual processing.

Chapter 6 aimed to investigate how colour signals are combined between the eyes, and whether there is evidence for monocular processing of colour in cortical visual areas. Functional MRI was used to measure BOLD activity while viewing LM-cone or S-cone isolating stimuli presented monocularly or binocularly. The results showed greater BOLD signal along ventral stream areas when stimuli were viewed binocularly in both the LM and S cone conditions. A region of interest analysis highlighted V1, V4, VO1, and VO2 as areas where there was a significant advantage to binocular viewing. This effect seemed to grow stronger in later visual areas, rather than weaker, although the binocular advantage was relatively small in all areas. This binocular > monocular advantage was only present for chromatic, and not achromatic stimuli. These results are consistent with the non-linear propagation of binocular > monocular differences due to the presence of monocular colour processing neurons in V1.

7.2 General Discussion

The research presented in this thesis demonstrates that chromatic adaptation can induce changes in hue perception which increase in magnitude beyond the timescale of photoreceptor adaptation (Rinner & Gegenfurtner, 2000). The observed adaptation aftereffects also persisted for at least five minutes after the removal of coloured filters, after which time photoreceptor adaptation recovery is generally considered to be complete. This suggested that the observed colour adaptation effects may be occurring at a post-photoreceptor stage of the visual system. However, the pattern of recovery did not align with previously reported long-term adaptation aftereffects, as there were no significant aftereffects present when tested at a 30-minute or a 60-minute timepoint post-adaptation. Even in the longest, 4-hour, adaptation condition, there was no evidence of significant hue changes 60 minutes post-adaptation, suggesting that adaptation recovery was complete within 60 minutes. Meanwhile long-term adaptation, which is assumed to be cortical, is characterised by enduring for many hours post-adaptation. This temporal profile therefore indicates that these effects may be part of a distinct 'medium-term' adaptation process. Adaptation at multiple temporal and hierarchical levels would enable the visual system to flexibly accommodate a large range of changes to the spectral properties of the environment, from abrupt shifts in light, to slow changes in ambient illumination, to gradual changes in the eye's physiology over the years.

One aim of this thesis was to investigate where in the visual system medium-term chromatic adaptation may occur. The observation that adaptation recovery occurs passively in the absence of de-adapting stimulation suggests that this adaptation is distinct from types of cortical adaptation that are maintained in darkness, such as motion aftereffects (Watamaniuk & Heinen, 2007). The lack of significant interocular transfer for colour aftereffects, even when the dichoptic adapting stimuli are matched in luminance, also implies an absence of binocular interaction in colour adaptation, which may imply a pre-cortical locus. However, this does not conclusively rule out a cortical contribution to medium-term chromatic adaptation. The results from Chapter 6 suggest that there are monocular populations of neurons present in V1 providing a plausible cortical site for adaptation that would not exhibit interocular transfer.

Another aim of the research in this thesis was to investigate the stage at which adaptation transitions from engaging short-term to long-term processes. Several studies report enduring effects after only 1-2 days of adapting to chromatic environments (e.g. Eisner and Enoch, 1982, Neitz *et al.,* 2002., Belmore and Shevell, 2008), which is suggested by Neitz *et al*. to be a cortical effect (Neitz *et al*., 2002). In Chapter 3, it was found that four hours of adaptation is not sufficient to induce these longer-lasting aftereffects. Furthermore, the effects of 60 minutes of adaptation were found to only occur monocularly, without any evidence of interocular transfer, further suggesting a pre-cortical locus. One interpretation of these findings is that long term cortical colour adaptation requires multi-day, repeated, adaptation to result in enduring effects. However, some researchers have failed to replicate the results shown by Neitz et al., contesting the very existence of long-term, multi-day adaptation. Eskew and Richters (2008) reported that they had been unable to induce shifts in unique yellow following long-term wearing of red-filtered lenses. The filters also did not change hue classification judgements or detection contours. Therefore, while this thesis has described four hours of adaptation as insufficient to induce long-term chromatic adaptation, it is important to acknowledge ongoing debate about whether this form of enduring adaptation can be reliably elicited at all.

One limitation of the psychophysical experiments performed in this thesis is that we did not control for practice effects or prior exposure to the colour-filtered environments. Several participants, including the experimenters, took part in multiple experiments in this thesis. Li et al. (2020) suggest that the visual system learns to adapt faster after repeated exposure to the same chromatic environment, and Engel et al. (2016) suggest that habitual wearers of coloured lenses show greater shifts of unique yellow after wearing the coloured lens. We would therefore predict greater adaptation aftereffects for participants who had repeatedly experienced the red or blue environments. However, the number of prior exposures to each filter was not systematically recorded or included in the analyses.

7.3 Future Directions

The question of whether medium to long term adaptation happens at a cortical site is still open. One method to try to investigate this further may be to design a paradigm to investigate it using neuroimaging techniques. While there has been some neuroimaging of short-term chromatic contrast adaptation, there has not been any study of longer-term adaptation. Studying this using neuroimaging techniques presents a problem due to the long amount of time needed for adaptation; it is not easy to enclose participants in MRI scanners for such a long time, for example. One potential paradigm that we considered for measuring the contribution of the cortex versus the retina to long term adaptation was to use ERG. ERG has previously been used to measure the L:M cone ratios in the retina (Neitz et al., 2008). We assume that a shift in unique yellow wavelength settings is expressed as a shift in L:M weighting. We can calculate the expected shift in L:M weightings to achieve the shift in unique yellow by comparing L:M sensitivity using ERG before and after adaptation. Any adaptation that is not explained by a shift in L:M sensitivity in the retina can be inferred to be occurring post-retinally. However, this is a difficult experiment to conduct, as the cone decrements from adaptation are relatively small compared to the normal variation of the L:M ratio between people, and the contrast that can be achieved while still isolating different cone types with silent substitution is limited. It was considered that the cone decrements that could be elicited by the experimental design may have been too small to be meaningfully separated from noise. Future researchers may wish to model the predicted cone decrements to establish if a signal to noise ratio could be achieved that would make this paradigm possible.

Another line of enquiry that was considered during this PhD but ultimately not completed due to time constraints was to investigate adaptation in colour anomalous individuals. A theory has emerged that long term adaptation processes may compensate for differences in the spectral tunings of cones for anomalous trichromats, meaning that the world appears more similar in colour to the perception of a colour normal observer than would be predicted from the cone absorption properties alone (e.g. Neitz, 2002). It has also been proposed that selective colour adaptation may be able to enhance colour discrimination for anomalous trichromats (Ro and Yang, 2004). Future research may wish to further investigate the idea that long term adaptation can be used to compensate for differences in cone spectral

tunings, as there could be applications in understanding the perceptual environment of colour anomalous individuals.

7.4 Overall Conclusions

This thesis shows that changes in the perception of colours that endure for at least five minutes can be induced through the wearing of coloured filters. The research supports the idea that colour adaptation goes beyond the timescale of a few seconds or minutes (as demonstrated by the classical view of short-term adaptation in cone photoreceptors), with the magnitude of colour adaptation aftereffects increasing for at least 15 minutes of adaptation, and suggests that the luminance of the environment, as well as the duration, can impact the magnitude of these aftereffects. As these colour aftereffects returned to baseline levels within 60 minutes after adaptation, this pattern of adaptation supports the idea of a ‘medium-term’ process which causes perceptual shifts that are larger and build up over a longer time than those caused by short-term colour adaptation, but is not as enduring as long-term colour adaptation. The lack of evidence for the maintenance of colour aftereffects by spending the recovery period in the dark, and the lack of evidence for interocular transfer effects, both suggest a possible pre-cortical locus of adaptation. However, the final study suggests that there are populations of single-input colour-sensitive neurons in V1, whose responses are disproportionately propagated throughout the ventral stream, which may provide a site for chromatic adaptation at a cortical level which would not display interocular transfer. Overall, this thesis characterises factors affecting medium-term colour adaptation, and investigates the binocular combination of colour in the cortex, speculating as to how this may affect our interpretation of the mechanisms underlying medium-term chromatic adaptation.

Appendices

Appendix 1: Variance of Unique Yellow and Unique Green

It is well established that unique green is a more variable measure than unique yellow, with UY being consistently set between 570-580nm (citations in Greene, 2024), but UG being set anywhere between 490-555nm (Schmidt et al., 2016). The results of Experiment 1 in Chapter 3 corroborate this variability. As a matter of interest, we have compared the variability of unique yellow (UY) and unique green (UG).

Comparing just the baseline values of UY and UG measured in the blue condition, the standard deviation of UY is 3.83 compared to 5.05 for UG. The minimum value recorded for UY was 562.78nm and the maximum was 580.76nm, giving a total range of 17.98nm difference across 11 participants. The minimum value of UG was 519.03nm and the maximum was 543.00nm, giving a range of 23.98nm.

Participants were also more individually variable when setting UG compared to UY in the blue filter baseline condition. The average standard deviation for UY across all baseline measurements was 2.37nm, whereas the average standard deviation for UG across all baseline measurements was 4.93nm, suggesting that UG is twice as variable as UY. For UY, participants' baseline variability across all baseline measurements was between 4.53nm and 11.02 nm, with the mean variation being 8.65nm. However, for UG, their variability across all baseline measurements was between 12.91nm and 24.15nm, with a mean variation of 17.96nm.

This variability could potentially impact the reliability of outcome measures relying on unique green; as such, unique yellow was used as the default outcome measure in the psychophysical experiments in this thesis.

Appendix 2: Code used to create LM/S stimuli in Chapter 6

```
#!/usr/bin/env python3
# -*- coding: utf-8 -*-
"""
Created on Tue Apr 25 12:16:13 2023

@author: jtm545

This script makes STLAB video files for use in the MRI experiments. Everything
is nicely paramatrised at the top of the script to make it easy to change bits.
"""
import sys
lib1 = '/groups/Projects/P1473/Code/PyPlr'
lib2 = '/groups/Projects/P1473/Code/PySilSub'
if not lib1 in sys.path:
    sys.path.append(lib1)
if not lib2 in sys.path:
    sys.path.append(lib2)

import os
import os.path as op
import random
import pickle

import numpy as np
import pandas as pd
import matplotlib.pyplot as plt
plt.style.use('bmh')
from pysilsub import waves, problems, observers
from pyplr import stlabhelp



# These are the conditions for the LMS and MEL blocks
LMS_CONDITIONS = ['MonRLMS', 'MonLLMS', 'BinLMS'] * 2
MEL_CONDITIONS = ['MonRMEL', 'MonLMEL', 'BinMEL'] * 2
SCONE_CONDITIONS = ['MonLScone', 'MonRScone', 'BinScone', 'BinScone']
LMINUSM_CONDITIONS = ['MonLLminusm', 'MonRLminusm', 'BinLminusm', 'BinLminusm']
COLOR_CONDITIONS = np.hstack(
    [LMINUSM_CONDITIONS, SCONE_CONDITIONS,
     LMINUSM_CONDITIONS, SCONE_CONDITIONS,
     LMINUSM_CONDITIONS, SCONE_CONDITIONS]
    )
FS = 50  # Effecitive sampling rate of two STLABs runnning together
BLOCK_DURATION = 360  # Length of block in seconds
```

```
BLOCK_TIME = np.linspace(0, BLOCK_DURATION, BLOCK_DURATION*FS)
ON_OFF_DURATION = 30  # Length of basic on/off component of design in ecopndss
OFF = np.zeros(ON_OFF_DURATION*FS)  # Zeros for off time points
ON = np.ones(ON_OFF_DURATION*FS)  # Ones for on time points
STIM_ON = np.hstack([ON, OFF])  # Full cycle for when the stim is ON
STIM_OFF = np.hstack([OFF, OFF])  # Full cycle for when the stim is OFF
LMS_PROBE_CONDITIONS = [1.0, 0.5, 0.25, 0.125]  # Probe contrast levels
LMS_PROBE_FREQUENCY = 4  # Hz
LMS_PROBE_DURATION = 1  # s
LMS_OFF = np.ones(len(BLOCK_TIME)) / 2
LMS_WAVE = waves.make_stimulus_waveform(
    frequency=LMS_PROBE_FREQUENCY,
    sampling_frequency=FS,
    duration=LMS_PROBE_DURATION
    )

# test data for s and lm mods
# s1_s_mod = np.ones((150,10))
# s2_s_mod = np.ones((150,10))
s1_lm_mod = np.ones((150,10))
s2_lm_mod = np.ones((150,10))


def make_flat(l):
    return [item for sublist in l for item in sublist]


def non_overlapping_ranges(n, width, low, high, spacing):
    """Find non-overlapping ranges for LMS probes.

    This is a brute-force method that will run indefinitely if
    overly-constrained.

    https://www.geeksforgeeks.org/python-non-overlapping-random-ranges/
    """
    ranges = set()
    for _ in range(n):
        candidate = random.randint(low, high - width)
        while any(candidate >= (idx-(width*spacing))
                  and candidate <= (idx + (width*spacing))
                  for idx in ranges):
            candidate = random.randint(low, high - width)
        ranges.add(candidate)
    ranges = [(idx, idx + width) for idx in ranges]
    return sorted(ranges)


```

```
92. def shuffle_conditions(left_stims, right_stims, conditions):
93.     """Shuffle the list of conditions."""
94.     shuffled = [(l, r, c) for (l, r, c)
95.                 in zip(left_stims, right_stims, conditions)]
96.     random.shuffle(shuffled)
97.     return zip(*shuffled)
98.
99.
100.
101.
102. def make_events(conditions, lms_probe_idxs, block_lms_probe_ids):
103.     cols = ['Onset', 'Event', 'Duration']
104.     binoff = ['BinOff']*6
105.     durations = [30]*6
106.     lms_durations = [1]*len(lms_probe_idxs)
107.     events = (
108.         pd.concat(
109.             [
110.                 pd.DataFrame(zip(range(30, 360, 60), binoff, durations), columns=cols),
111.                 pd.DataFrame(zip(range(0, 360, 60), conditions, durations), columns=cols),
112.                 pd.DataFrame(sorted(zip([l[0]/50 for l in lms_probe_idxs],
['LMS']*len(lms_probe_idxs), lms_durations, block_lms_probe_ids)), columns=cols+['ProbeID'])
113.              ]
114.             ).sort_values(by='Onset').reset_index(drop=True)
115.         )
116.     return events
117.
118.
119.
120.
121. def make_vf_data(profile, low_spec, high_spec):
122.     data = (
123.         np.vstack(
124.             [low_spec if s==0 else high_spec for s in profile]
125.             ) * 4095
126.         ).astype('int')
127.     return data
128.
129.
130. def insert_time_col(data):
131.     return np.hstack([BLOCK_TIME[:, np.newaxis]*1000, data])
132.
133.
134.
135. def add_attention_events(conditions, idxs):
136.     #breakpoint()
137.     new_conditions = []
```

```
    new_event_times = []
    for c, i in zip(conditions, idxs):
        new_cons = c + ['Attention']
        new_idxs = i.copy()
        while new_cons[0] == 'Attention' or new_cons[-1] == 'Attention':
            random.shuffle(new_cons)
        for list_idx, event in enumerate(new_cons):
            if event == 'Attention':
                low = new_idxs[list_idx-1][1]
                high = new_idxs[list_idx][0]
                val = random.randint(low, high)
                attention_idx = (val, val+20)
                new_idxs.insert(list_idx, attention_idx)

        new_conditions.append(new_cons)
        new_event_times.append(new_idxs)

    return make_flat(new_conditions), make_flat(new_event_times),


def make_colour_conditions():
    conditions = []
    event_idxs = []
    for block in range(12):
        tadd = block*1500
        if block % 2 == 0:
            lminsum = LMINUSM_CONDITIONS.copy()
            random.shuffle(lminsum)
            conditions.append(lminsum)
        else:
            scone = SCONE_CONDITIONS.copy()
            random.shuffle(scone)
            conditions.append(scone)
        #idxs = non_overlapping_ranges(4, 150, 50, 1420, 1.5)
        idxs = [(i, i+150) for i in colour_ranges()]
        idxs = [(val[0]+tadd, val[1]+tadd) for val in idxs]
        event_idxs.append(idxs)
    #conditions = [c for sublist in conditions for c in sublist]

    return conditions, event_idxs


def plot_colour_block(conditions, idxs):
    fig, axs = plt.subplots(2, 1, figsize=(12, 4))
    axs[0].plot(np.ones(18000)/2, lw=3, c='k')
    axs[0].set_ylabel('Right eye')
    axs[1].plot(np.ones(18000)/2, lw=3, c='k')
```

```
    axs[1].set_ylabel('Left eye')
    axs[1].set_xlabel('Time (ms)')
    for c, i in zip(conditions, idxs):
        r = range(i[0], i[1]+1)
        if c == 'Attention':
            axs[0].vlines(r, .2, .5, color='k', lw=.1)
            axs[1].vlines(r, .2, .5, color='k', lw=.1)
        if c == 'MonLScone':
            axs[1].vlines(r, 0, 1, color='blue', lw=.05)
        if c == 'MonRScone':
            axs[0].vlines(r, 0, 1, color='blue', lw=.05)
        if c == 'BinScone':
            axs[0].vlines(r, 0, 1, color='blue', lw=.05)
            axs[1].vlines(r, 0, 1, color='blue', lw=.05)
        if c == 'MonLLminusm':
            axs[1].vlines(r, 0, 1, color='purple', lw=.05)
        if c == 'MonRLminusm':
            axs[0].vlines(r, 0, 1, color='purple', lw=.05)
        if c == 'BinLminusm':
            axs[0].vlines(r, 0, 1, color='purple', lw=.05)
            axs[1].vlines(r, 0, 1, color='purple', lw=.05)

    for ax in axs:
        ax.set_ylim((0, 1))
        sep = range(0, 18001, 1500)
        for s in sep:
            ax.vlines(s, 0, 1, color='k', lw=.5)

    return fig


def make_colour_events(conditions, idxs):
    cols = ['Onset', 'Event', 'Duration']
    onset = [i[0]/50 for i in idxs]
    duration = [(i[1]-i[0])/50 for i in idxs]
    events = pd.DataFrame(zip(onset, conditions, duration), columns=cols)
    return events


def colour_ranges():
    onsets = np.arange(93, 1108, 336)
    onsets = np.array([o + random.randint(-17, 18) for o in onsets])
    return onsets

def test_colour_ranges():
    while True:
        r = colour_ranges()
```

```
        assert r[0] >= 75
        assert r[1] - r[0] > 300
        assert r[2] - r[1] > 300
        assert r[3] - r[2] > 300
        assert r[3] <= 1425
        print('Fine')

def colour_block(block_dir, age=32, scone_angle=1.5, lm_angle=2.386):

    # Peak contrasts for s and lm cone conditions
    peak_s = .4
    peak_lm = .09

    cons, idxs = add_attention_events(*make_colour_conditions())
    events = make_colour_events(cons, idxs)
    events.to_csv(op.join(block_dir, 'events.csv'))
    fig = plot_colour_block(cons, idxs)
    fig.savefig(op.join(block_dir, 'block.png'))

    # Load the lms spectra for each device
    with open('./stims/STLAB_1_background.pkl', 'rb') as file:
        s1bg = pickle.load(file)

    # Load the melanopsin spectra for each device
    with open('./stims/STLAB_2_background.pkl', 'rb') as file:
        s2bg = pickle.load(file)

    # Make the mods
    obs = observers.ColorimetricObserver(32, 10)
    S1 = problems.SilentSubstitutionProblem.from_json('./calibration/STLAB_1_York.json')
    S2 = problems.SilentSubstitutionProblem.from_json('./calibration/STLAB_2_York.json')
    S1.background = s1bg
    S2.background = s2bg
    S1.observer, S2.observer = obs, obs

    x = waves.make_stimulus_waveform(
        frequency=2,
        sampling_frequency=50,
        phase=0,
        duration=3,
    )

    # Scone
    for problem in [S1, S2]:
        problem.target = ['sc', 'mc', 'lc', ]
        problem.silence = ['mel']
        problem.ignore = ['rh']
```

```
279.         problem.do_gamma(fit='polynomial')
280.     # TODO: add calibration value for S-cone here
281.     s1_solutions = []
282.     s2_solutions = []
283.     target_contrasts = x * peak_s
284.     for target_contrast in target_contrasts:
285.         S1.target_contrast = [target_contrast * np.sin(scone_angle),
286.                               target_contrast * np.cos(scone_angle)/np.sqrt(2),
287.                               target_contrast * np.cos(scone_angle)/np.sqrt(2)]
288.         s1_solutions.append(S1.linalg_solve())
289.
290.         S2.target_contrast = [target_contrast * np.sin(scone_angle),
291.                               target_contrast * np.cos(scone_angle)/np.sqrt(2),
292.                               target_contrast * np.cos(scone_angle)/np.sqrt(2)]
293.         s2_solutions.append(S2.linalg_solve())
294.
295.     s1_sc_mod = pd.concat([pd.Series(S1.gamma_correct(s)) for s in s1_solutions],
axis=1).T.values
296.     S1.background = s1_sc_mod[0]
297.     s2_sc_mod = pd.concat([pd.Series(S2.gamma_correct(s)) for s in s2_solutions],
axis=1).T.values
298.     S2.background = s2_sc_mod[0]
299.
300.     # Lminusm
301.     for problem in [S1, S2]:
302.         problem.target = ['mc', 'lc']
303.         problem.silence = ['sc', 'mel']
304.         problem.ignore = ['rh']
305.     # Code here for lminusm stuff
306.
307.     s1_solutions = []
308.     s2_solutions = []
309.     target_contrasts = x * peak_lm
310.     for target_contrast in target_contrasts:
311.         S1.target_contrast = [target_contrast * np.sin(lm_angle), target_contrast *
np.cos(lm_angle)]
312.         s1_solutions.append(S1.linalg_solve())
313.
314.         S2.target_contrast = [target_contrast * np.sin(lm_angle), target_contrast *
np.cos(lm_angle)]
315.         s2_solutions.append(S2.linalg_solve())
316.
317.     s1_lm_mod = pd.concat([pd.Series(S1.gamma_correct(s)) for s in s1_solutions],
axis=1).T.values
318.     S1.background = s1_lm_mod[0]
319.     s2_lm_mod = pd.concat([pd.Series(S2.gamma_correct(s)) for s in s2_solutions],
axis=1).T.values
```

```
320.     S2.background = s2_lm_mod[0]
321.
322.
323.     # Make the stim profiles
324.     left = np.array([s1bg for i in range(18000)])
325.     right = np.array([s2bg for i in range(18000)])
326.
327.     for c, i in zip(cons, idxs):
328.         r = range(i[0], i[1])
329.         if c == 'Attention':
330.             left[r] = left[r] * .5
331.             right[r] = right[r] * .5
332.         if c == 'MonLScone':
333.             left[r] = s1_sc_mod
334.         if c == 'MonRScone':
335.             right[r] = s2_sc_mod
336.         if c == 'BinScone':
337.             left[r] = s1_sc_mod
338.             right[r] = s2_sc_mod
339.         if c == 'MonLLminusm':
340.             left[r] = s1_lm_mod
341.         if c == 'MonRLminusm':
342.             right[r] = s2_lm_mod
343.         if c == 'BinLminusm':
344.             left[r] = s1_lm_mod
345.             right[r] = s2_lm_mod
346.
347.     left = insert_time_col(left)
348.     right = insert_time_col(right)
349.
350.     left_vf = pd.DataFrame(left, columns=stlabhelp.get_video_cols()).astype('int')
351.     right_vf = pd.DataFrame(right, columns=stlabhelp.get_video_cols()).astype('int')
352.
353.     # Make video files
354.     left_vf_name = op.join(block_dir, 'colour_left.json')
355.     right_vf_name = op.join(block_dir, 'colour_right.json')
356.
357.     stlabhelp.make_video_file(left_vf, left_vf_name)
358.     stlabhelp.make_video_file(right_vf, right_vf_name)
359.     #breakpoint()
360.     return left_vf_name, right_vf_name, events,
361.
362.
363. if __name__ == '__main__':
364.     if not op.exists('./test'):
365.         os.mkdir('./test')
366.     #melanopsin_block('./test')
```

```
367.     #lms_block('./test')
368.     colour_block('./test')
369.
370.
```

Appendix 3: Left vs Right Eye fMRI Analysis

One consideration for the significant activity found in Chapter 6 in the binocular > monocular conditions could be on account of the blind spot. When measuring the eyes separately, there will be a point in visual cortex corresponding to the blind spot in the measured eye which will therefore not respond at all. When the eyes are stimulated together, the sections of visual cortex corresponding to the blind spot to each eye are stimulated by the opposite eye. Therefore, for a full-field stimulus, we would expect to find activity corresponding to the blind spots in the binocular condition that is not present in the monocular condition, and so could potentially account for the finding of greater activity in the binocular condition in some regions. Although the size of the stimulus (15º radius) means the blind spot for most people would be at the very edge of the stimulus, and therefore may not impact results, we tested the possibility by running an analysis to contrast the activity from the left eye with the activity from the right eye.

Statistical analysis was conducted using FEAT. Four regressors were investigated: LM left eye, LM right eye, S left eye, and S right eye. These regressors were constructed by convolving the stimulus presentation timings with a canonical double gamma haemodynamic response function (HRF) waveform. The resulting general linear model was applied at each voxel to identify significant BOLD responses.

An exploratory whole brain analysis was conducted using FEAT. Participants' functional data were transformed to MNI space and combined across participants using a second level mixed-effects analysis in FLAME for two contrasts: LM left – right, and S left - right.

The results (shown in Figures A3.1 and A3.2) suggest that there is no significant activity in visual areas corresponding to the location of the blind spot in either the LM or S cone conditions for the left eye – right eye contrast. The small amount of scattered activity in non-visual areas is likely to be spurious. We conclude that the binocular > monocular activity reported in Chapter 6 is not due to the impact of the blind spot.

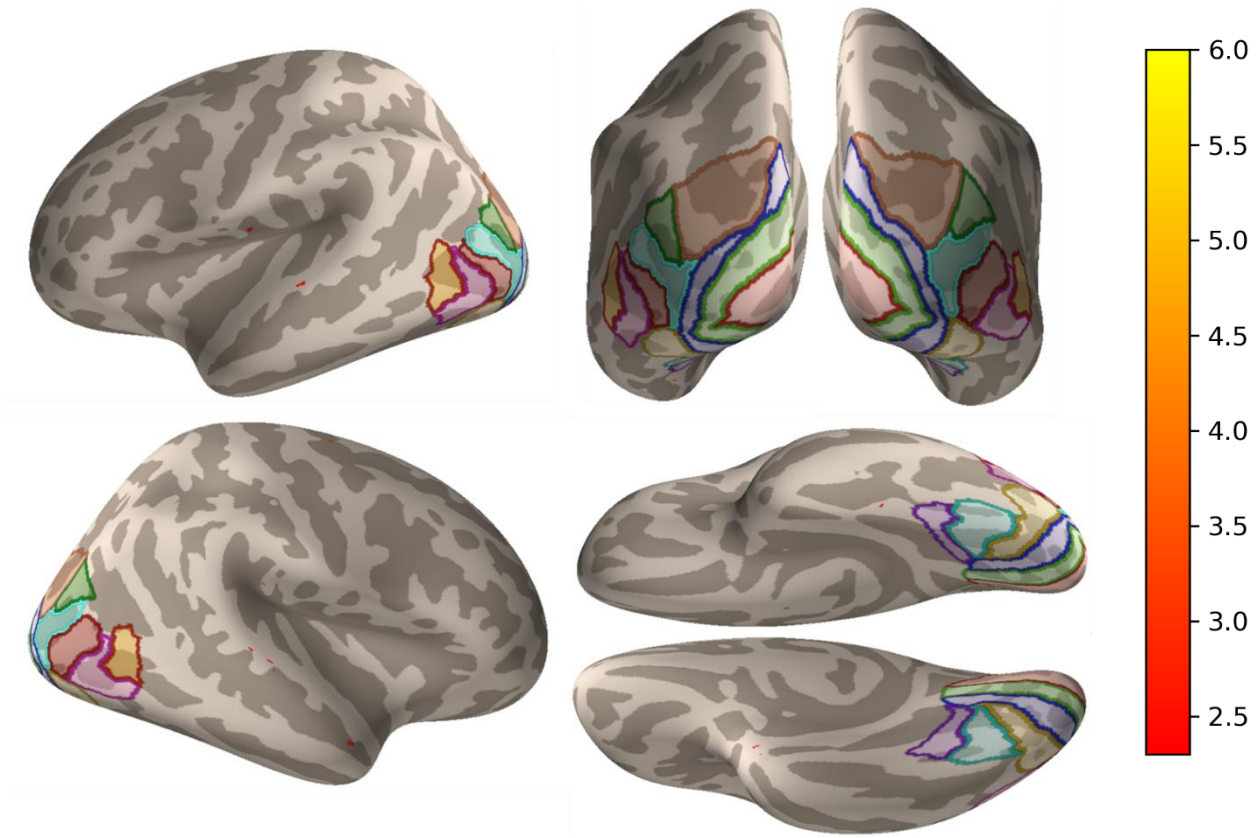


Figure A3.1: *Thresholded and cluster corrected z-stat (2.3) for the left eye – right eye contrast in the LM condition*

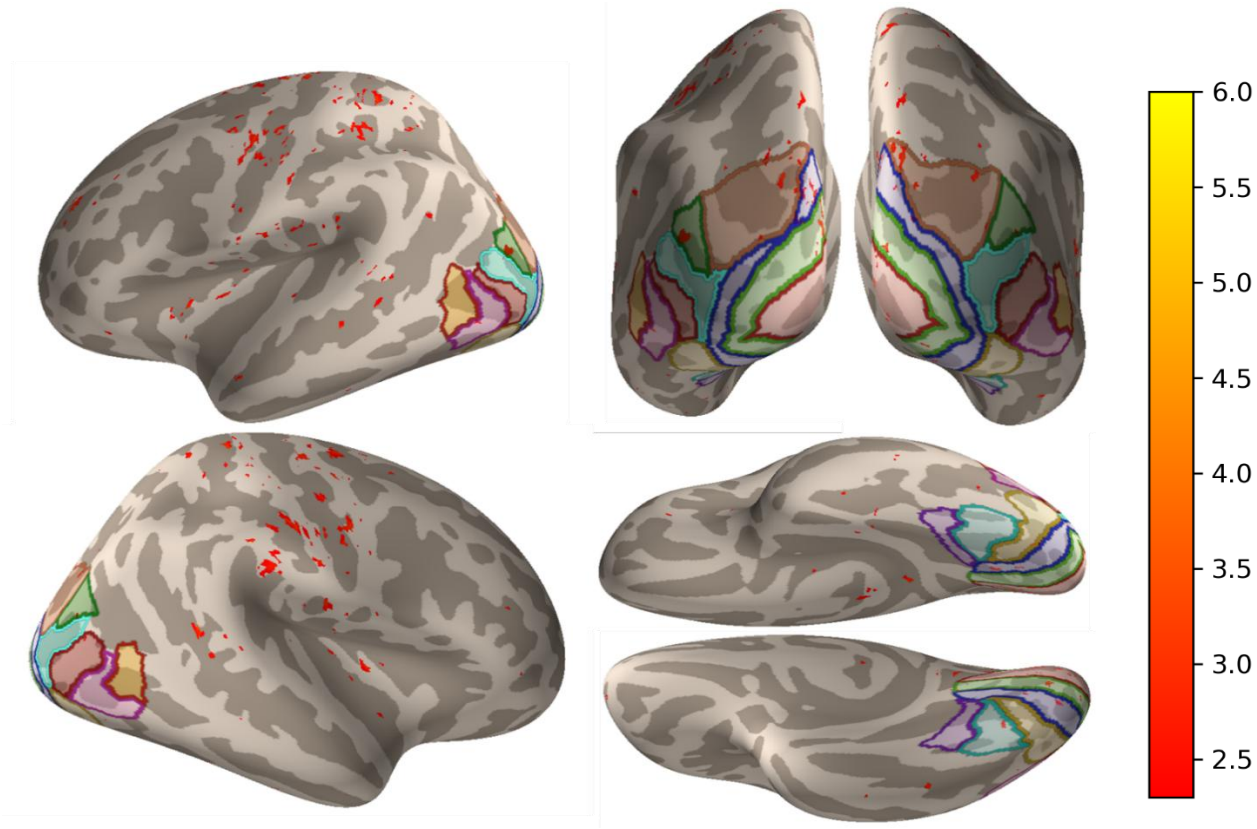


Figure A3.2: *Thresholded and cluster-corrected z-stat (2.3) for the left eye – right eye contrast in the S cone condition.*

Appendix 4: Correlation of monocular and binocular responses within individuals

To check how well an individual's monocular response correlated with their binocular response, monocular mean beta values were plotted against binocular mean beta values, and a linear model was fitted across the data, for each ROI with significant binocular > monocular activity (see Figure A4.1). The intercepts are shown in Table A4.1. Gradients near 1 suggest that participants' monocular and binocular responses are near-perfectly correlated. In other words, the binocular advantage observed in the region should be equal across participants. In all ROIs in both conditions, regression slopes are near 1. For ROIs with a regression slope above 1, participants whose monocular responses are higher experience a greater binocular advantage compared to those whose monocular responses are lower.

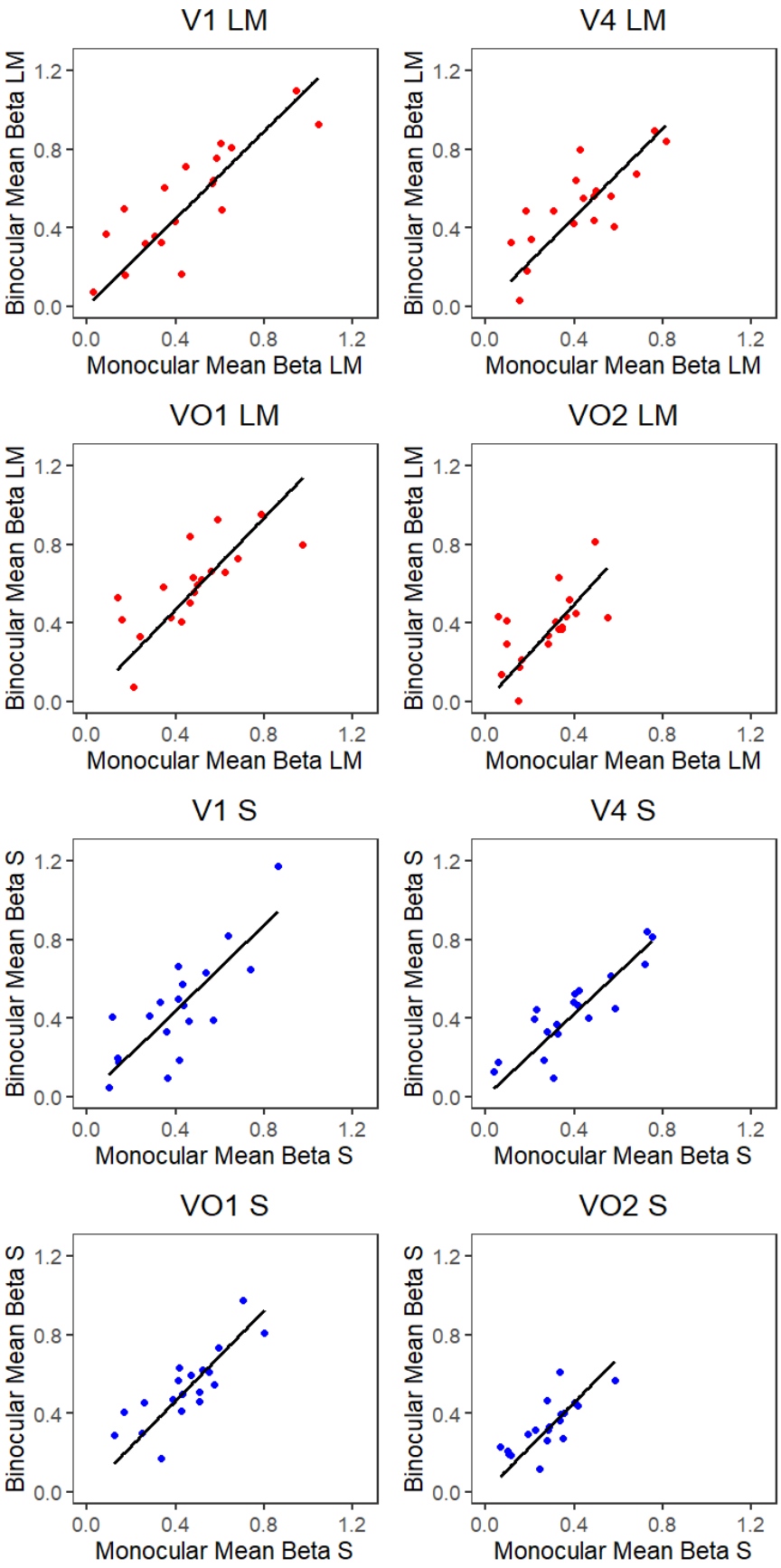


Figure A4.1: *Monocular versus binocular mean beta response for LM and S cones. Lines represent a linear model with intercept (0,0).*

Table A4.1: *Gradients for each cone class in each ROI with significant binocular > monocular activity.*

ROI	Cone	Gradient
V1	LM	1.11
	S	1.09
V4	LM	1.13
	S	1.05
VO1	LM	1.17
	S	1.15
VO2	LM	1.24
	S	1.14

Appendix 5: Binocular combination of achromatic stimuli measured with fMRI

As part of a separate project run concurrently with the project reported in Chapter 6, data were collected on the binocular integration of achromatic-isolating and melanopsin-isolating stimuli. For the purposes of comparison with the results presented in Chapter 6, the results of the binocular > monocular contrast for achromatic stimuli are presented here.

In this experiment, stimuli were presented monocularly or binocularly via the Spectra Tune Lab multiprimary devices and liquid light guides described in Chapter 2 and Chapter 6. Stimuli were projected onto a circular diffuser for each eye with a field size of 30 degrees of visual angle, with the central 7 degrees of visual angle masked. Stimuli selectively isolated either the L+M luminance channel, or melanopsin photoreceptors. Participants therefore either saw achromatic discs flickering between black and white, or melanopsin modulations which are largely not consciously detectable, although some participants reported a sensation of flicker corresponding to the stimulus.

Eighteen participants (aged 18-60) were tested using a similar fMRI procedure to that previously reported. The stimuli were presented in a block design, with a block duration of 360s, with a 30s off / 30s on design. The conditions used were: monocular left melanopsin, monocular right melanopsin, binocular melanopsin, monocular left LMS, monocular right LMS, binocular LMS. The stimulus blocks were presented in a random order. Attentional probes were used but had four contrast levels (1, 0.5, 0.25, 0.125), and were present for 1 second.

Data analysis was conducted using FEAT from FSL. The following contrasts were analysed: monocular melanopsin, monocular LM, binocular melanopsin, binocular LMS, binocular melanopsin > monocular melanopsin, binocular LMS > monocular LMS. The results reported here are solely for the binocular LMS > monocular LMS contrast.

The unthresholded z-stats for the binocular > monocular contrast for the LMS condition are contrasted with the unthresholded z-stats for the LM and S conditions in Figure A5.1. This shows that the ventral stream activity in this contrast to LM and S cone stimuli is absent in the LMS condition.

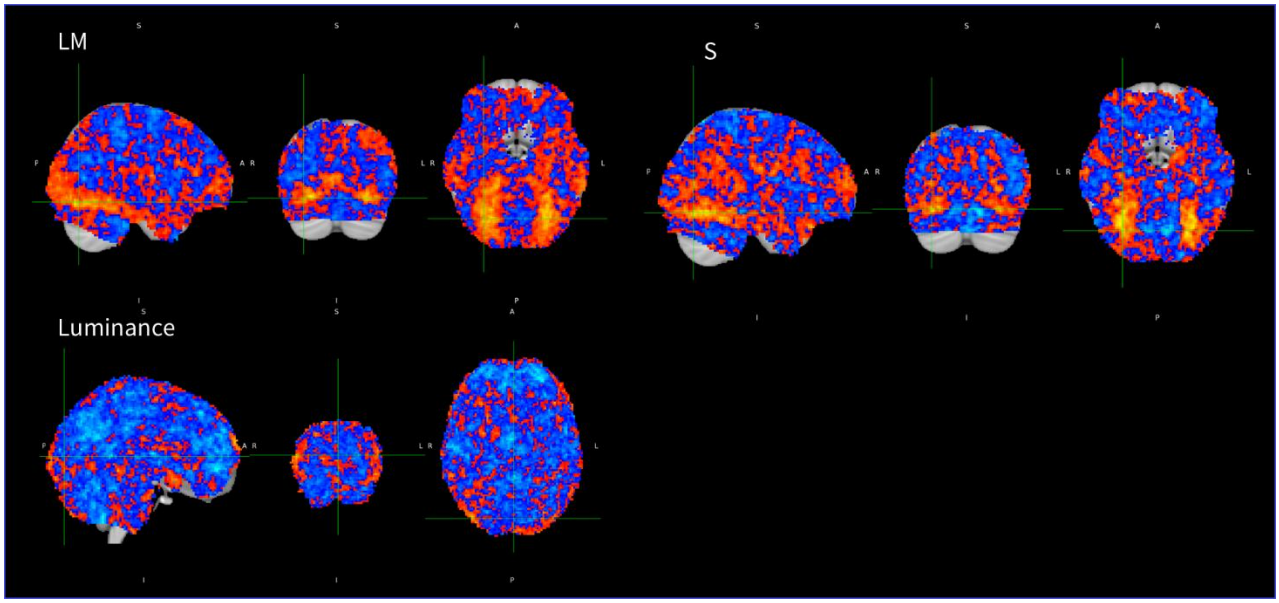


Figure A5.1: *Unthresholded z-stats for binocular > monocular contrast in the LM, S, or LMS conditions.*

Figure A5.2 shows the LMS binocular > monocular z-stat thresholded at 1.96, plotted on a freesurfer fsaverage inflated brain using pysurfer. There is no significant activity in any visual areas.

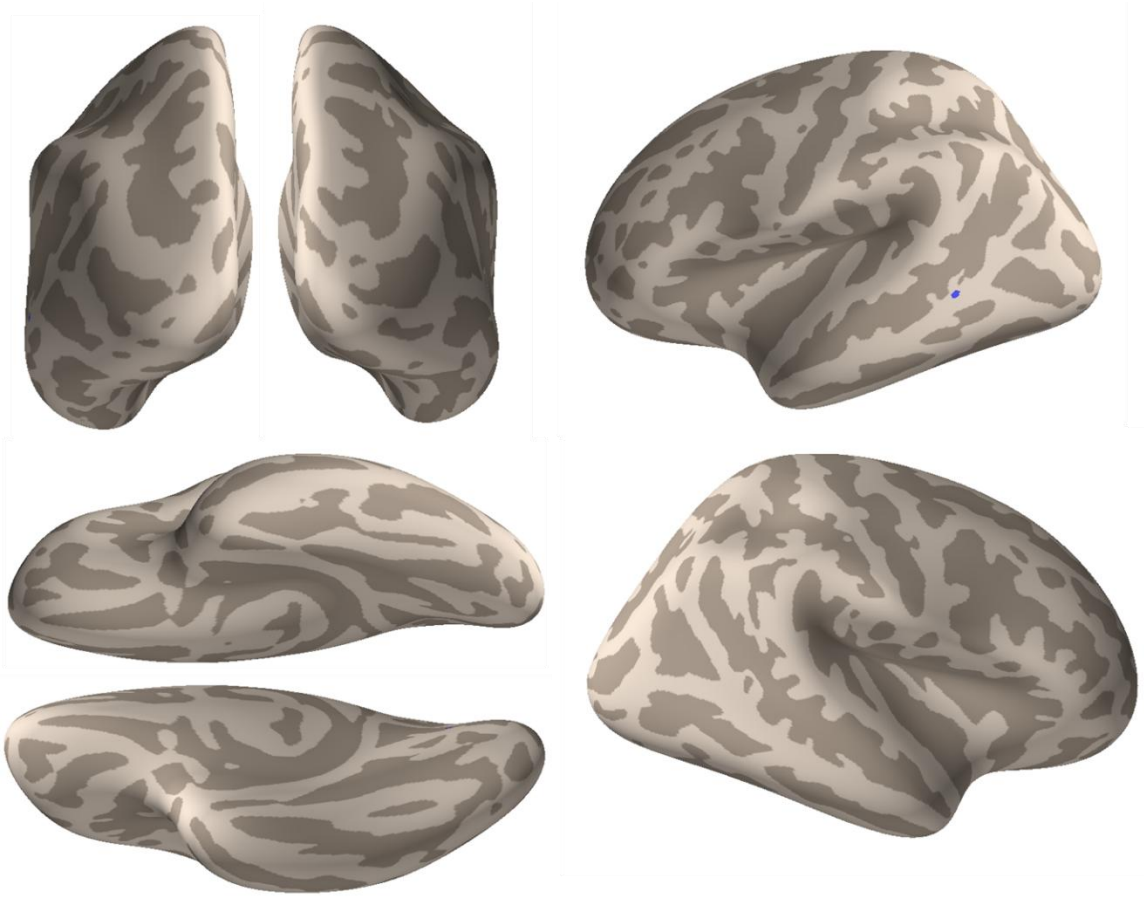


Figure A5.2: *Thresholded and cluster-corrected z-stat (1.96) for LMS binocular > monocular contrast (n = 18)*

These results support the claim that the binocular > monocular activity reported in Chapter 6 is specific to coloured stimuli and is not seen for achromatic stimuli.

Appendix 6: Use of R packages in analysis

For computational transparency, as well as to acknowledge and cite analysis packages, I list here any packages used in my data analysis, on top of base R (R Core Team, 2023).

ANOVAs were performed using the function aov_ez from the package afex (Singmann et al., 2024).

Correlations were performed using the function cor from the package stat (Bolar, 2019).

Gaussian mixed effect modelling was performed using the package mclust (Fraley et al., 2024).

Linear models were performed using the package lme4 (Bates et al., 2025).

Dplyr was used for data transformation and manipulation (Wickham et al., 2023).

Plots were created using the packages ggplot2, ggpubr, ggthemes, and paletteer (Arnold et al., 2024; Kassambara, 2023; Wickham et al., 2025).

Bayes Factor analyses were conducted using JASP (JASP Team, 2024).

Appendix 7: Use of Generative AI

In accordance with university policy on the use of generative AI (as of June 2025), I record here all use of ChatGPT-4 to assist me in any way with the production of this thesis (OpenAI, 2025).

Date	Nature of Use
27/02/2025	MATLAB to R code conversion
10/03/2025	Coding debugging
14/03/2025	Coding debugging
17/03/2025	Statistical analysis/coding (prompt related to how to perform Gaussian mixed effect modelling)
20/03/2025	fMRI analysis troubleshooting (prompt related to possible issues to explain poor registration)
25/03/2025	Statistical analysis/coding (prompt related to best way to code linear models in R)
10/04/2025	Coding debugging
21/04/2025	fMRI analysis (prompt related to the syntax for creating ROI maps using freesurfer)
22/04/2025	Coding debugging
24/04/2024	fMRI analysis (prompt related to the difference between binarized or non-binarized ROI maps)
28/04/2025	fMRI analysis troubleshooting (prompt related to realigning some misaligned ROI maps)
02/05/2025	Coding debugging
07/05/2025	Proof-reading
14/05/2025	Coding debugging
30/05/2025	Coding debugging
02/06/2025	Coding debugging
16/06/2025	Coding debugging
20/06/2025	Proof-reading
02/07/2025	Coding debugging
07/07/2025	Proof-reading

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