ANOMALOUS TRICHRROMACY:
EXTERNAL ENHANCEMENT OF COLOUR SIGNALS,
INDIVIDUAL DIFFERENCES AND DIAGNOSIS

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Thesis submitted for the degree of Doctor of Philosophy

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I hereby declare that this thesis has not been and will not be, submitted in whole or in part to another university for the award of any other degree. The thesis conforms to an ‘article format’ in which the first chapter presents an introductory overview chapter of the relevant literature, an outline of the empirical work of the thesis, and discussion of the overall contribution of the thesis to the field. The remaining chapters consist of three papers written in a style appropriate for publication. All three are in preparation for journal submission.

Signed:
Chapters and author contributions

Chapter 1 provides an overview of the relevant literature, introducing concepts, theories, a summary of the papers included in this thesis and their overall contributions.

Chapter 2 is written in a style appropriate for the Journal of Vision, in UK English:

Somers, L., Bosten, J. Modelling the effectiveness of EnChroma notched filters for improving colour vision in anomalous trichromacy.

Author contributions: LS and JB designed the research, LS collected and analysed the data, LS and JB wrote the paper.

Chapter 3 is written in a style appropriate for the Journal of Vision, in UK English:


Author contributions: LS and JB designed the research, LS collected and analysed the data, LS and JB wrote the paper.

Chapter 4 has been written in a style appropriate for the Journal of the Optical Society of America A, in UK English:

Somers, L., Bosten, J. Recommendations for screening for mild anomalous trichromacy using the Ishihara Plates test.

Author contributions: LS and JB designed the research, LS collected and analysed the data, LS and JB wrote the paper. Undergraduate Lily Winney assisted with a portion of the recruitment process.
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COVID-19 impact statement

In early 2020 the COVID-19 pandemic was declared, and by March the first lockdown came into force. The University of Sussex campus was closed, halting any in-person activity including experimental testing. At this time, I was in the early stages of data collection for a project which would have formed a chapter in this thesis; an electrophysiological investigation of post-receptoral compensation of colour vision signals in anomalous trichromats. This project involved a novel method of recording electrophysiological responses to colour from the retina and visual cortex simultaneously, to identify changes in the scaling of chromatic signals between those two stages of the visual system. Data collection had already been pushed close to the end of my PhD by the substantial period of preliminary experimentation needed to establish the parameters of the experiment, and by the extensive population screening needed to identify the special population being researched. Once in-person activity had been suspended there was no way to continue with data collection. The data from ten control participants and two experimental participants were analysed but not included in this thesis.

COVID-19 has significantly impacted my original research and has altered the scope of my thesis, but I believe the research included forms a cohesive and compelling body of work, and I intend to resume the affected projects after completing the PhD.
Summary

Anomalous trichromacy is known to conceal a substantial range in perceptual ability, but this is not typically considered in assessments of corrective aids and diagnostic tests. In addition to the diversity caused by genetic polymorphisms, perceptual ability is thought to be influenced by little understood postreceptoral mechanisms, adding to the need for research focusing on this population.

A modelling and behavioural investigation establishes the effectiveness of EnChroma filters in enhancing anomalous colour vision. Paper 1 (not yet published) employs a physiologically accurate model of colour vision to estimate the enhancements in cone-opponent signals conferred by the filters. Paper 2 (not yet published) presents behavioural validation of the model’s predictions, showing that notch filters can result in enhanced perceived saturation for deuteranomalous observers, with effects for suprathreshold perception and partial effects at absolute threshold.

Paper 3 (submitted for publication) uses the physiologically accurate model of colour vision to investigate the impact of variation in edition and lighting conditions on the effectiveness of the Ishihara plates test in identifying those with mild anomalous trichromacy. The model predicts a significant impact of plate and illuminant, but no influence of edition, which is supported by the findings of a behavioural investigation.

This thesis provides the first direct evidence that altering the input to the visual system using filter-based aids can impact the cone-opponent signals available to anomalous trichromats, and that this change in signal is useable by the visual system, resulting in changes to perceived saturation.
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Chapter 1 - Introduction & Thesis Overview

1.0 Introduction

The evolution of trichromatic colour vision allowed primates to distinguish colour differences that were indistinguishable to those without three-dimensional colour vision, e.g., fruit in amongst foliage, the colours of predators, and likely countless other discriminations that improved their chances of survival (Carvalho et al., 2017). From then, colour has played a part in every facet of life, contributing to visual skills such as visual search, object recognition, and to the complex phenomena of preference (Hurlbert & Ling, 2007), culture (Albers et al., 2020), and language (Regier & Kay, 2009). Colour vision is a highly detailed sense, allowing the discrimination of around 2.3 million colours (Linhares et al., 2008a) from the responses of just three wavelength specific photoreceptors. However, colour vision does not have this level of detail for all observers, with around 8% of the human male population (and about 0.4% of the female population) possessing some form of colour vision deficiency (Birch, 2012). There is a wide range of perceptual abilities within colour vision deficiency (Bosten, 2019), and although those with more severe anomalies experience more greater detrimental effects, mild anomalies can lead to their own impacts. Those with mild anomalies may be able to benefit from a greater range of corrective devices than severe anomalies (Salih et al., 2020), but the effectiveness of these interventions is disputed. Mild anomalies are also harder to identify, as they are vulnerable to screening error (Birch, 1997b) which may contribute to the mildest of anomalies being underrepresented in research and undiagnosed in the community.
1.1 Colour vision: physics and physiology

1.1.1 Spectral power distributions of light
Light refers to the portion of the electromagnetic radiation spectrum that is visible to humans due to light sensitive cells in our retinas. When arranged according to wavelength, visible light ranges from roughly 380 to 700 nm. Colour vision describes the ability to differentiate spectra of light according to their distributions of energy at different wavelengths (rather than intensity differences where spectra differ at all wavelengths by the same factor), and so work investigating colour vision deals with light in terms of spectral power distributions (SPDs). This is a way of describing the amount of energy at each wavelength.

Most objects are seen by reflecting a proportion of light emitted from a light source, where the light interacts with the surface molecules of an object, with some of this energy absorbed, and the unabsorbed energy reflected into the eye. As such, the spectral power distribution of light reflected from an object is the SPD of the illuminant multiplied by the surface reflectance spectrum (the proportion of light reflected at each wavelength). This spectrum of the illuminant may be complicated by ambient light or inter-reflections from other surfaces in the scene. Some objects fluoresce, where some energy from the non-visible range is converted into visible light (and therefore the proportion of light ‘reflected’ at some, or all wavelengths may be greater than 1).
1.1.2 Cones
In normal trichromatic vision the retina contains three classes of cone photoreceptor which are named according to the wavelengths they are most sensitive to, as long (L), medium (M) and short (S) wavelength sensitive classes. The sensitivity of a cone indicates the likelihood of a photon reaching the cone being absorbed. Each photoreceptor class has a roughly Gaussian sensitivity curve across a region of the spectrum, with sensitivity at a minimum at the edges, climbing to a peak near the middle of the receptive range. S cones are maximally sensitive at ~420 nm, M cones at ~530 nm and L cones at ~560 nm. In line with the principle of univariance (Mollon, 1989), individual cone classes confound wavelength and intensity, and it is only by comparison to a cone class with a sensitivity rage that is different but overlapping, that wavelength information be extracted.

The sensitivity of a cone class is determined by its opsin, a heptahelical protein encoded by individual opsin genes for the L, M and S cone classes (Sharpe et al., 1999). The absorption of a photon of a wavelength within the opsin’s sensitive range causes it to change from an 11-cis-retinal isomer to an all-trans-retinal isomer. This isomerisation begins a signalling cascade that leads to a change in electrical potential which is passed on to the connected cells in the retina.

The three classes of cone are intermingled in a quasi-random mosaic (Mollon & Bowmaker, 1992; Roorda & Williams, 1999). S cones are the least common cone class, are almost completely absent from the fovea for a diameter of 0.15° (Curcio et al., 1991), and form around ~7% of all cones in the periphery (Curcio et al., 1991). On average, there are about twice as many L cones as M cones in the retina (Vos & Walraven, 1971).
However, there is great variation between individuals, with proportions of L to M cones found to vary from 1.1:1, to 16.5:1 without any appreciable impact on colour discrimination (Hofer et al., 2005). Individual differences in cone class proportions impacts perceptual isoluminance. The perception of brightness is based on the combined activity of the L and M cones, and individual differences in L:M ratio cones gives different weightings to the two regions of the spectrum into the luminance signal.

1.1.3 Retinal architecture
The retina consists of layers of cells found at the rear of the eye, separating the vitreous fluid of the inner eye from the pigmented choroid. The retina covers the entirety of the rear surface of the eye, with the density of retinal cells sparser at the outer edges where it meets the ciliary bodies holding the lens. The rod and cone receptors are positioned in a single layer, arranged in a mosaic individual to each retina. L and M cone densities peak at the fovea, responsible for fine detailed vision. Receptors are absent at the blind spot where the optic nerve leaves the eye.

Neurons of the retina can be classified into five main types: the photoreceptors (rods and cones) which absorb photons and pass signals to the bipolar cells which compare the activities of neighbouring photoreceptors via indirect connections with horizontal cells. Ganglion cells receive signals from bipolar cells and are the output cells of the retina. Amacrine cells are a second class of laterally connected cell that modify signals between the bipolar and ganglion cell layers. Adding complexity to the five main cell types are many cell subtypes: there are at least 10 types of bipolar cell, 20 ganglion cell types and between 30 and 40 amacrine cell types (Dacey, 2000).
1.1.4 Cone opponent mechanisms in the retina

Two colour channels arise from cone opponency between different classes of cone, also referred to as the cardinal colour mechanisms. The L/(L+M) opponent channel compares L and M cone activities and its often referred to as the ‘red/green’ channel, despite representing colour variation from cherry to teal (Abramov & Gordon, 1994; Jameson & D’Andrade, 2009). The S/(L+M) opponent channel represents comparisons between S cone activity and the combined activities of L and M cones. This is frequently referred to as the “blue/yellow” channel but represents colour variations from violet to chartreuse (Abramov & Gordon, 1994; Jameson & D’Andrade, 2009).

The L/(L+M) opponent channel is carried by midget ganglion cells which feature a centre-surround antagonism between L and M cone activities (Martin, 1998). Midget cells are categorised as either ON- or OFF- depending on whether they are excited or inhibited by activity of the cones feeding the centre of their receptive fields. Red ON-midget cells are excited by L cone activity at the centre of their receptive fields but inhibited by input to the surround. This surround input was previously believed to consist of the opposing cone class, but increasing evidence suggests non-selective combination of cone classes (Diller et al., 2004; Wool et al., 2018). The spatial segregation of a distinct centre and surround of the receptive field means that midget ganglion cells likely contribute to spatial edge-detection as well as carrying chromatic information (Conway, 2001). The size of midget ganglion cell receptive fields is small, with the smallest receptive fields identified in the midget cells serving the central retina, which take input from as few as a single cone cell to the receptive field centre (Dacey & Petersen, 1992; Diller et al., 2004).
Small bistratified ganglion cells carry the second opponent colour channel, comparing S cone activity to combined L and M cone activity, or S/(L+M), representing chromatic information along a violet to chartreuse axis. These cells do not show centre-surround antagonism, being activated by S cone activity and inhibited by combined L and M cone activity within the same non-spatially selective receptive field (Patterson et al., 2019).

Parasol ganglion cells encode luminance by combining inputs from L and M cones, also showing spatial antagonism between excitatory and inhibitory regions of the receptive field. Parasol cells are named after their distinctly large receptive fields, which gives the resulting representation of luminance contrast a low spatial resolution (Dacey & Petersen, 1992).

1.1.5 Colour in the Lateral Geniculate Nucleus

The signals carried along physiologically distinct colour-opponent channels project to physically separate layers of the Lateral Geniculate Nucleus (LGN, Chatterjee & Callaway, 2003). The midget cells project to the parvocellular layers of the LGN (Dacey, 1999), and the small bistratified ganglion cells project to the koniocellular layers (Hendry & Reid, 2000). Information about achromatic luminance contrast is carried by parasol ganglion cells projecting to the magnocellular layers (B. Lee, 2008), but also by the midget cells projecting to the parvocellular layers. These layers are retinotopic: each region of the visual field is aligned congruently in each layer, with a greater proportion of each layer dedicated to foveal vision than to the periphery (Schneider et al., 2004).
1.1.6 Colour in the cortex

The processing of colour is not associated with a single region of the cortex but spread across a network of regions (Gegenfurtner, 2003; Solomon & Lennie, 2007). The first cortical region that processes colour is V1. Colour processing in V1 has been linked to cytochrome oxidase blobs, with more colour-tuned cells found within the blobs than outside them (Livingstone & Hubel, 1984) and also within the thin layers of strips in V2 (summarised in Gegenfurtner, 2003).

In contrast to the LGN, there appear to be relatively few neurons tuned to respond to colour in the occipital cortex, with those that do responding to multiple visual features, such as orientation and spatial frequency as well as colour (Grill-Spector et al., 1998). Despite the occipital cortex not exclusively responding to colour, there are few occipital areas that show no response to colour, and particularly strong responses to colour occur in V1 and in the ventral occipital cortex (Mullen, 2019). Many of the individual neurons tuned to colour show tunings that span a broad range of colours (Gegenfurtner, 2003; Solomon & Lennie, 2007). While colour processing in the LGN is segregated into two cardinal axes, there are neurons in the cortex (V1, V2, V3, V4) that respond to intermediate hues (Gegenfurtner, 2003; Kuriki et al., 2015). Single cell recordings in primates have identified the organisation of cells tuned to specific hues to be similar across multiple cortical regions, including V1 (Xiao et al., 2007), V2 (Lim et al., 2009) and V4 (Li et al., 2014). Neurons responding to specific hues have been identified in partially overlapping clusters, with each cluster representing a full gamut of hue in a small cortical area (Xiao et al., 2007). It is thought that there are cortical areas specialised for the processing of colour such as V4 (Zeki & Marini, 1998), and V8 (Hadjikhani et
Investigations into primate cortical colour processing at a single cell level has revealed most colour coding cells in V1 to be double-opponent, an extension of the single-opponent midget cells and parvo cells in the retina and the LGN (Conway, 2001). In double opponent cells the opponency of cells found in the LGN is inherited for the receptive field centre, but reversed for the surround, for example the central receptive field of this type of cell may show excitatory input from L cones and inhibitory input from M cones, with the reverse inputs to the surround. This double opponency is thought to be part of the basis of colour constancy, the visual system’s ability to discount changes in illuminant to retain a stable percept of colour (Hurlbert, 2003, 2007). One theory states that colour constancy is achieved through invariance in cone activities (Foster & Nascimento, 1994) in relation to surface edges, therefore requiring tuning for spatial chromatic edges that double opponent cells could provide (Hurlbert & Wolf, 2004; Kraft & Brainard, 1999).

1.2 Historical development of theories of colour vision
1.2.1 Trichromatic theory
Isaac Newton (1642-1727) contributed the first step towards the modern understanding of light by demonstrating that the colours commonly observed when shining white light through a prism were fundamental and indivisible qualities of light. Leonhard Euler (1707-1783) first attributed colours to the wavelengths of light (Euler, 1787), explaining that colour was determined by the wavelength of light in the same way that pitch is
determined by the wavelength of sound, also noting that the chromatic appearance of surfaces was defined by surface reflectance. The idea that colours were created by a continuous spectrum of wavelengths, as “wave theory” defended by Newton and Euler, was held in direct conflict with the known ability to mix all colours from three primaries (Mayer, 1758). This demonstrable trichromatic colour mixing was taken as evidence that there were three distinct categories of light (Mayer, 1758). It wasn’t until Thomas Young proposed that trichromacy was due to the eye containing three light sensitive ‘particles’ (Young, 1802), that the “wave theory” of chromatic light could be seen to coexist with the trichromacy of colour mixing, but even then, it was many decades before the notion was accepted (B. Lee, 2008). Hermann von Helmholtz developed the theory further, proposing that the eye contained three types of colour sensitive nerves in the retina which were “short-[wavelength] preferring”, “middle-prefering” and “long-prefering”, with the percept of hue arising from the comparison of signals from each, and the intensity of the hue percept relating to the amount of stimulation of each nerve type (Maxwell, 1871). James Clerk Maxwell contributed behavioural evidence in support of the Young-Helmholtz theory of trichromacy, using a spinning top to create the first example of modern colour matching experiments (Maxwell, 1857). Maxwell’s spinning top experiments were cited as the direct ancestor of the colour matching experiments of Wright (Wright, 2007). By the late 1800’s our modern understanding of the physiological basis of trichromacy, and the potential of colour matching experiments were firmly established.
1.2.2 Opponent theory
For many years idea of trichromacy put forward by Young and Helmholtz were held in conflict with the opponent theory advocated by Hering (1834-1918), who suggested there were four colours with 'unique' status, forming two of the three colour opponent mechanisms: red-green, blue-yellow and black-white (Hering, 1878). Evidence for these colour-opponent mechanisms was sparse, aside from the aphoristic impossibility a yellowish blue or a reddish green (B. Lee, 2008). The conflict between trichromacy and opponent process theory was partly resolved when Hurvich and Jameson combined them into a two-stage “dual process theory” of colour vision (Hurvich & Jameson, 1957). This model combined the three cone classes of the Young/Helmholtz theory as the first stage, with a second stage of opponent processing that would permit Hering’s opponent pairs: red/green, blue/yellow and black/white. Shortly after this proposal, L vs M “on” and “off” cells were discovered, appearing to provide a physiological basis for Hering’s colour-opponent pairs (de Valois et al., 1966; Wiesel & Hubel, 1966). However, the ability for this to provide an explanation for unique red and green percepts was undermined by psychophysical experiments that found the colour axis represented by these retinal cells to be tuned to red-teal rather than red-green (Jameson & D’Andrade, 2009). An equivalent population subserving a “blue/yellow” mechanism was also identified (Dacey & Lee, 1994), but this was found to be tuned to a “chartreuse-violet” axis (Jameson & D’Andrade, 2009). The neural basis of Hering’s unique hues remains to be determined as they are not the colours the retinogeniculate colour opponent mechanisms are tuned to. Despite this difference, current theories of colour vision support both trichromacy and opponent process theory.
1.2.3 Colour vision deficiency
Noted Chemist John Dalton drove a lot of scientific interest in colour vision deficiency (CVD), through his precise descriptions of his own vision. He realised when he began working in the field of botany in 1790 his difficulty in identifying certain specimens by their colour. Dalton published his first paper discussing CVD including a theory that his abnormal colour vision was caused by a colouring of his ocular media to filter out red light (Dalton, 1794). Dalton bequeathed his eyes to science, and upon a self-directed post-mortem his theory was disproven. Young posited soon after that colour vision deficiency may be due to the deficiency or absence of one of the colour sensitive mechanisms in the eye (Young, 1807). One of Daltons’s eyes was luckily left intact, and, much later and in accord with Young’s conjecture, (D. M. Hunt et al., 1995) were able to use DNA analysis to find that John Dalton was in fact a dichromat lacking M cones; a deuteranope.

Dalton was not the first to note a colour vision deficiency, with anecdotal reports of renaissance painters struggling to distinguish colours (Lanthony, 2001). Early discussion of the phenomenon was hampered by a lack of consensus in terminology, with “dichromatic” coexisting with the same referred to as “dichromic” and “Daltonic” (Balaraman, 1962). Early attempts to classify individuals with colour vision deficiency were made by a number of prominent researchers across Europe (Purkinje, 1828; Seebeck, 1837; Szokalski, 1841; Wartmann, 1846; Wilson, 1855), with Seebeck (1837) gaining the most attention for his use of the first formal screening tests (B. Lee, 2008).
1.3 Specifying colour: colorimetry and colour spaces

The study of colour relies on having accurate ways to define, communicate and replicate colour. The creation of numerical definitions of colour is referred to as colorimetry, which has enabled the standardisation, to the end that observers of the same type can be presented with a colour of the same specifications under the same conditions and receive the same perceptual information. Many colour spaces have been developed, each specifying colour in different ways, reflecting the purpose of its use and the restrictions this use acts under.

The earliest and simplest colour spaces reflected the knowledge of the time. Newton’s colour scale was derived with reference to the octave scale, whereas Goethe’s colour wheel refers to colours as personal attributes, and Mayer’s colour triangle was developed amid theoretical struggles to reconcile the trichromacy of colour mixture with the continuous spectrum of light (B. Lee, 2008). Helmholtz’s colour space was derived from colour matching experiments to determine complementary spectral colours, and Hering’s colour space was defined by opponent axes, with intermediate colours defined as mixtures of the four poles (B. Lee, 2008).

Many contemporary colour spaces have taken the three colour attributes identified by Grassmann: hue, saturation, and lightness as the foundation of colour description. This convention of describing colour by three attributes means that work primarily focussed on chromaticity is often done using colour spaces which discard the dimension relating to luminance variation, using two axes to present an isoluminant plane of all chromaticities, such as the CIE xy space described in Section 1.3.1, or the MacLeod Boynton chromaticity diagram described in Section 1.3.2.
Colour spaces differ in the values used to define colour, some are physical, and are tied to objective stimuli, others are termed perceptual, and relate to colour as it is experienced. Separate physical and perceptual colour spaces are required because colour vision is non-uniform. When presenting colour in a physically uniform space, such as defining colour by wavelength, the amount of perceptual change between equivalent distances differs across the space. This is referred to as a perceptual nonuniformity. Attempts to define a perceptually uniform space are described in Section 1.3.3.

1.3.1 CIE colour spaces
The Commission Internationale de l’Eclairage (CIE) is an organisation which was formed in 1913 to forward the scientific and technological work in the field of light by forming internationally agreed standards for the research community to follow. In 1931 the CIE endorsed the XYZ space as a valid demonstration of the link between wavelengths of light and perceived colours (Wright, 2007). The wavelengths in nanometres (nm) have known locations along the convex spectrum locus (the boundary defining the outer extremity of possible colours). It is a physical rather than perceptual colour space, so the distances within the space relate to linear changes in the physical colour, rather than difference in colour percept.

These colour spaces were based on the values identified in separate colour matching experiments by Wright and Guild (Guild, 1931; Wright, 1929). Using three monochromatic lights as primaries, Wright and Guild requested observers to adjust these primaries until a match was obtained to a series of test monochromatic lights. The colour matching functions resulting from the measurements of Wright and Guild were found
to be so similar that they were amalgamated and form the CIE 1931 RGB colour matching functions which are still in use. At some points in the spectrum, it is only possible to create a match when one of the primaries is added to the test light, resulting in negative values in the RGB matching functions.

The CIE XYZ space was a transformation of the RGB values of the colour matching function into a single set of entirely positive values, that preserved the algebraic additivity required by Grassmann’s laws, and that described the overall sensitivity captured by the luminous efficiency function, $V(\lambda)$. The xyY chromaticity space has two chromatic dimensions ($x=X/(X+Y+Z)$, $y=Y/(X+Y+Z)$) and $Y$ (which is $V(\lambda)$, where each plane of constant $Y$ is an isoluminant colour space (Fairman et al., 1997).

A key limitation of the XYZ, and xy, space is its lack of perceptual uniformity, which results in equal distances at different points in the space equating to different magnitudes of perceptual change. This non-uniformity was demonstrated by the discrimination measurements of MacAdam in 1942, giving weight to the need for a perceptually uniform space to formally represent colour appearance. In 1976 the CIE accepted CIE-$L^*a^*b^*$ and CIE-$L'u'v'$ spaces, for their approximate perceptual uniformity and their ability to be derived from the CIE XYZ space using a small number of simple mathematical transforms. In both cases the $L$ is a luminance dimension, and $a^* b^*$ or $u'v'$ are chromatic dimensions. With the $L^*a^*b^*$ space, $a^*$ and $b^*$ approximate the Hering opponent colour dimensions, the $a^*$ from green (decrement) to red (increment), and the $b^*$ from blue (decrement) to yellow (increment). While both spaces are designed to approximate human vision, neither achieve true perceptual uniformity.
These and later spaces proved invaluable for the calculation of device-independent representation of colour on digital screens. Later variations, such as CIECAM97 and CIECAM02 were based on later colour matching experiments and feature more complex models of chromatic adaptation and non-linear visual processing, in order to achieve improved perceptual uniformity (Moroney et al., 2002).

1.3.2 The MacLeod Boynton chromaticity diagram

The MacLeod Boynton chromaticity diagram (MacLeod & Boynton, 1979) is a colour space based on the S, M and L cone fundamentals, in which the two ‘cardinal’ axes represent the two cone-opponent processes. The ordinate represents a trade-off between L and M cone activations, denoted by the ratio $L/(L+M)$. Though a common misnomer refers to this as the red-green axis, it more accurately refers to chromatic variation from cherry to teal (also see Section 1.1.4). As the M cone activation contributes to the denominator, the scale starts on the left with the highest M cone contribution, progressing in decrement to an achromatic point, then on in increments of L cone activation. The abscissa represents a trade-off between S cone activity and activity in the other two cone types and is denoted by the ratio $S/(L+M)$. Although this axis is commonly referred to as the blue/yellow axis, it represents chromatic variation from violet to chartreuse (Section 1.1.4), with the smallest S cone activation represented at the bottom of the diagram increasing as you move up. As this chromaticity diagram directly represents the cone opponent processes, it is useful for modelling retinogeniculate neural representations of colour, and colour vision anomalies. As the S
cones do not contribute to luminance, this axis is arbitrarily scaled, the implication being that the scales on the two axes cannot be considered equivalent.

1.3.3 Munsell colour space
The Munsell colour space is distinct from colour spaces mentioned thus far as it is not derived from colour matching functions or cone fundamentals, but from perceptual judgements of colour. Each of the colours represented in the space were selected for their subjective colour appearance. By building the space based on appearance, the space achieves approximate perceptual uniformity, meaning that across the space, the same distance refers to the same degree of difference in colour appearance. It features three axes, hue, chroma and value, with the hue circle varying by degrees around the vertical scale of value, and lightness from black to white. Distance from this central vertical pole denotes chroma, with levels of chromatic intensity increasing with distance from the achromatic centre. The extremity of the space is irregular to account for differing peaks in chroma for different hues at different values.

The Munsell colour system was developed by Albert Munsell as a rational notation of colour to use in his teaching. The first full version was published in “A Color Notation” (Munsell, 1905), which was developed into the Munsell Book of Color (Munsell, 1929). Extensive experimentation contributed to the development of the modern Munsell Book of Colour (Judd, 1940), which is available as a book of physical removable colour surfaces. Because the printing is highly controlled and the surfaces are deemed to be highly lightfast, the Munsell surfaces are used extensively in visual psychophysics experiments which require uniform physical stimuli.
The Munsell system has been refined since the original handmade publications in 1929, with an extensive range of occupation-specific chromatic scales targeted towards environmental colour communication, such as the Munsell Soil Color Book (X-Rite, Baltimore, MD USA, 1975), as well as research and design focused colour control with the master atlas, The Munsell Book of Color, Glossy edition (X-Rite, 2018). The reflectance spectra of the full 1600 surface set of Munsell colour chips are available online (sites.uef.fi/spectral) and are a valuable resource for vision research.

1.4 Individual differences in colour vision
1.4.1 Causes of differences in colour vision
The most severe forms of colour vision deficiencies are congenital, which cause a stable deficiency throughout the affected individual’s lifetime. Congenital colour vision deficiencies disproportionately affect the L/(L+M) channel as the L and M cone classes are particularly vulnerable to genetic mutations (Simunovic, 2010). The genetics of congenital colour vision deficiencies will be presented in Section 1.4.2.

The time course and severity of acquired defects varies greatly and is dependent on the cause of the defect. CVD acquired as a side effect from medication is typically milder and more transient than CVD acquired though systemic or ocular pathology, with acquired defects disproportionately affecting the Tritan, or S/(L+M) channel (Simunovic, 2016). Colour Vision deficiency can be acquired as a result of chronic illnesses such as Alzheimer’s disease, diabetes mellitus, glaucoma, leukaemia, liver disease, multiple sclerosis, Parkinson’s disease, sickle cell anaemia and retinitis pigmentosa (Hasrod & Rubin, 2016). Medications for malaria, rheumatoid arthritis, psychosis, epilepsy,
congestive heart failure, hypertension and erectile dysfunction have been found to induce deficiencies of discrimination of S-cone stimuli, while antidepressants and antituberculotic medications have been found to induce deficiencies of colour discrimination along the L/(L+M) axis (Hasrod & Rubin, 2016). Senescent changes in the ocular media lead to reductions in S cone sensitivity, through the yellowing of the lens or by changes in macular pigment density (Salvi et al., 2006). For a thorough review of acquired CVD see Simunovic (2016).

1.4.2 Genetics of colour vision deficiency
In normal trichromatic vision, the sensitivities of the cones are determined by the opsin proteins encoded by the opsin genes OPN1LW (L cone), OPN1MW (M cone), and OPN1SW (S cone) (J. Neitz & Neitz, 2011). OPN1LW and OPN1MW are arranged in a tandem array on the X-chromosome, and share 98% of their nucleotide sequence, in comparison to their ~40% homology to OPN1SW (J. Neitz & Neitz, 2011). This indicates that OPN1LW and OPN1MW evolved comparatively recently (Nathans et al., 1986), and due to their high homology, are prone to unequal recombination (J. Neitz & Neitz, 2011), where the genes are misaligned during meiosis resulting in errors during crossing-over. The location of the gene array on the X-chromosome explains why CVD is more common in men than women (see Section 1.4.5). Men express abnormal L or M opsin genes carried on their single X-chromosome, while women with one affected X-chromosome will express normal opsin genes carried by the unaffected X-chromosome in half of cone cells (due to X-chromosome inactivation: (Lyon, 1961) and therefore typically not show CVD.
When this mispairing is intergenic, and an opsin gene crosses over with an intergenic region, the result is deletion of a gene (Sharpe et al., 1999). The deletion of an OPN1MW gene, leaving functional OPN1SW and OPN1LW genes, results in deuteranopia, and the deletion of OPN1LW, leaving functional OPN1SW and OPN1MW genes, results in protanopia. When the mispairing is intragenic, meaning sections of an OPN1LW gene cross over with sections of an OPN1MW gene, this concatenation results in a hybrid opsin gene, which, when expressed, creates a cone class with a spectral sensitivity somewhere between those of ‘normal’ M and L cones (Sharpe et al., 1999). The spectral sensitivity of each opsin is encoded by the amino acids at certain positions within the gene (Chen et al., 1989; Kosower, 1988). The L and M opsin genes have 6 exons. Two loci in exon 5 are responsible for most of the difference in spectral sensitivity between the human L and M cone pigments. Loci in exons 2, 3 and 4 make smaller contributions to shift spectral sensitivity, and exons 1 and 6 do not contribute to spectral sensitivity (J. Neitz & Neitz, 2011).

A traditional view is that normal trichromacy is subserved by the presence of normal L, M and S cone opsins, and anomalous trichromacy arises when a ‘hybrid’ anomalous opsin featuring a concatenation of two normal opsins presents alongside a normal L or M cone (Rushton et al., 1973). However, a consequence of the frequent intermixing of the L and M opsin genes is that variation in amino acid sequences is present among individuals with normal colour vision, in addition to those with anomalous colour vision. For example, a common polymorphism found among normal trichromats is the presence at site 180 in the L opsin of either serine, L(ser180), or alanine, L(ala180), with a respective 63:37 split in prevalence (Stockman et al., 2000; Figure 1). The population
supports a number of variants of the M and L opsin genes, and normal trichromatic
colour vision is conferred by any pair of opsins providing a sufficient difference in
spectral sensitivity (Drummond-Borg et al., 1989). An alternative view of the genetic
basis of anomalous trichromacy is that rather than being based on separate ‘hybrid’
opsins not present in the population of normal trichromats, anomalous trichromacy
occurs where any pair of opsin genes (that are also expressed in normal trichromacy)
confers substantially smaller than normal photopigment spectral separation.
Other genetic mutations are known to cause colour vision deficiencies in less common cases (J. Neitz & Neitz, 2011). For example, the combination of 5 amino acids referred to as LIAVA (Leicine153, Isoleucine171, Alanine174, Valine178, Alanine180 in exon 3) has a deleterious effect on whichever opsin gene it occurs in, resulting in none of that opsin being expressed (Mizrahi-Meissonnier et al., 2010; M. Neitz et al., 2004). Other mutations have been found to prevent opsinps from forming functional photopigments or prevent the opsin gene from being transcribed (J. Neitz & Neitz, 2011).

1.4.3 Classes of congenital colour vision deficiency

1.4.3.1 Dichromacy

Dichromacy occurs when one cone class is absent, resulting in colour discrimination based on the comparison of signals from 2 cone classes. The absence of L cones results in protanopia which effectively removes the L/(L+M) channel and reduces the luminance of longer wavelengths of light (Sharpe et al., 1999). The absence of M cones results in deuteranopia, also eliminating the L/(L+M) channel. The absence of S cones results in the much rarer tritanopia, which eliminates the S/(L+M) subsystem, restricting chromatic discrimination to a comparison of the activities of the L and M cone classes. Some dichromats are able to make trichromatic colour discriminations of large field stimuli, potentially due to a small number of ‘residual’ cones of the ‘missing’ type being present in the retinal periphery (Sharpe et al., 1999). A deuteranope, for example, may have genes for two different M class opsinps encoded on the x chromosome, with a small
number of the second class expressed due to proximity between the opsin gene and the locus control region (Sharpe et al., 1999).

1.4.3.2 Anomalous trichromacy

Anomalous trichromacy occurs when colour vision is subserved by three classes of cone in the retina, but where the strength of available colour signals is reduced. The majority of anomalous trichromacy is X-linked, in which the spectral sensitivities of the cone classes sensitive in the medium and long wavelength parts of the spectrum are more similar to one another than in normal trichromacy (J. Neitz & Neitz, 2011). In the case of deuteranomaly, the M cone class is replaced by an anomalous cone class (which I refer to as L'), with a spectral sensitivity far closer to that of the normal trichromatic L cone than that of the normal trichromatic M cone (Bosten, 2019). The deuteranomalous observer therefore has a retina with three classes of cone: S, L' and L. In the case of protanomaly, the L cone is replaced by an anomalous cone class, M', with a spectral sensitivity far closer to that of the normal trichromatic M cone than that of the L cone (Bosten, 2019). The protanomalous observer has a retina with three cone classes: S, M and M'.

The severity of an individual case of anomalous trichromacy is defined in terms of the spectral separation between the peaks in sensitivity of the two X-linked cone classes, referred to as the delta lambda max, or $\Delta\lambda_{\text{max}}$ (DeMarco et al., 1992). The greater the $\Delta\lambda_{\text{max}}$ the greater the signal diversity and signal to noise ratio of the L/(L+M) channel (Mollon, 1989). There is great variation in the severity of X-linked anomalous trichromacy, with different variants conferring a $\Delta\lambda_{\text{max}}$ of between 1 and 12 nm, compared
to the ~30 nm available to normal trichromats (Bosten, 2019). Cases of anomalous trichromacy with minimal $\Delta \lambda_{\text{max}}$ result in only residual red-green discrimination and are sometimes referred to as extreme anomalous trichromats, (Simunovic, 2010). Although the $\Delta \lambda_{\text{max}}$ defines the strength of the available chromatic signals, it does not correlate well with perceptual ability (Bosten, 2019), which is thought to be influenced by the absolute peaks in spectral sensitivity (He & Shevell, 1995), variation in the densities of ocular media of the eye (Thomas et al., 2011) and by compensatory postreceptoral mechanisms discussed further in Section 1.9.2.

Tritanomaly occurs when an anomalous variant of the S cone is present instead of the normal S cone. Unlike X-linked anomalous trichromacy, this does not affect the spectral sensitivity of the cone class but causes a reduction in the functionality of the photopigment (Deeb & Motulsky, 2013; Zabel et al., 2021).

1.4.3.3 Rare forms of congenital colour vision deficiency

Monochromacy is an extremely rare group of colour vision deficiencies in which only one cone type (or no cones and only rods) is available, resulting in no ability to discriminate colour. Most cases are either rod monochromacy or blue cone monochromacy.

Blue cone monochromacy is X-linked, usually triggered when genetic mutations affect the locus control region (LCR) located upstream of the L and M opsin gene array, preventing the expression of the L and M opsins, leaving only S cones and rods (Deeb & Motulsky, 2013). This rare disorder results in poor visual acuity and photophobia as well as severely reduced colour discrimination. L cone monochromacy arises from genetic
mutations deleteriously affecting the M and S cones, leaving vision to be supported by L cones and rods. M cone monochromacy arises from genetic mutations deleteriously affecting the L and S cones, leaving vision to be supported by M cones and rods. In cases where the retina has only one functioning class of cone, rods contribute a second dimension of colour discrimination at low light levels, enabling colour discrimination comparable to that of dichromats (Deeb & Motulsky, 2013; Reitner et al., 1991). L and M cone monochromacy are the rarest forms of monochromacy, affecting less than 1 in 1,000,000 of the population (Simunovic, 2010), as these deficiencies require two separate deleterious genetic mutations (Sharpe et al., 1999).

Rod Monochromacy is an autosomal recessive congenital disorder causing the dysfunction of all three cone types leaving vision dependant on the rods (Deeb & Motulsky, 2013). People with rod monochromacy suffer severe photophobia in photopic conditions, long-sightedness, nystagmus and scotoma in addition to their total colour blindness (Deeb & Kohl, 2003). Worldwide 1 in 30,000 suffer from rod monochromacy, but in certain populations with a restricted gene pool the prevalence is higher, for example between 6 and 10% of Pingelapese Islanders suffer from rod monochromacy (Simon et al., 2004).

1.4.4 Variation within normal trichromacy
While anomalous colour vision is attributed to insufficient difference between the spectral sensitivities of the X-linked cone types, normal trichromatic colour vision is maintained by the presence of two X-linked cone types with a sufficient spectral separation between their sensitivities (Bosten, 2019). Rather than normal trichromatic
colour vision occurring in the presence of “normal” L and M cones, frequent unequal recombination events have led to a diversity of cone opsins found within the normal trichromatic population (Deeb & Kohl, 2003). These polymorphisms play a role in variation in normal trichromacy as well as in anomalous red-green colour vision and have been linked to individual differences in colour matching (Sanocki et al., 1993).

Women who are heterozygous for CVD carry the genes expressed in CVD as well as those expressed in normal trichromacy. Most such heterozygotes have normal colour vision, but some heterozygotes have been found to exhibit mild abnormalities in colour matching and discrimination (Jordan & Mollon, 1993). Females show X-chromosome inactivation, expressing one X-Chromosome randomly in every cell (Lyon, 1961). Female heterozygote carriers of CVD therefore have a retina that is a patchwork of cones that normally confer both CVD and normal trichromacy. For carriers of anomalous trichromacy this results in a retina that contains four cone classes (Jordan & Mollon, 2019). Discrimination depends on the delta lambda maxes of the pairs of cone types present: in rare instances, tetrachromatic colour vision may be supported (Jordan & Mollon, 2019).

1.4.5 Prevalence of colour vision deficiency
The prevalence of red-green colour vision deficiencies differs between men and women because the OPN1MW and OPN1LW genes encoding the M and L opsins are on the sex-linked X chromosome. Only homozygous women, those who have inherited two abnormal alleles, have CVD (Birch, 2012). Large studies of prevalence have shown that some form of CVD affects ~8% of men and ~0.4% of women (Birch, 2012). The
prevalence of sex-lined X chromosomal traits in females can usually be predicted from the prevalence in males, which in the case of CVD predicts a prevalence of \(0.08^2\) 0.64% in females, which is greater than the rate observed. The cause of this discrepancy has been identified as the fact that women heterozygous for two different colour vision deficiencies will present both. For example, for heterozygous carriers of protanomaly and deuteranomaly the spectral separation between \(L'\) and \(M'\) cones can be great enough to confer trichromatic colour vision within the normal range, and consequently these individuals are not classed as anomalous trichromats by tests for CVD (Jordan & Mollon, 1993).

Deuteranomaly is the most common type of CVD, affecting 4.63% of men, and 0.36% of women. Deuteranopia affects 1.27% of men and 0.01% of women (Sharpe et al., 1999), protanomaly 1.08% of men and 0.03% of women, and protanopia 1.01% of men and 0.02% women (Sharpe et al., 1999). Tritan (S-cone) deficiencies appear at equal rates between the sexes as OPN1SW is located on an autosomal chromosome. Tritan deficiencies are rarer than other forms of CVD, with estimates of prevalence ranging from \(~0.005\%\) (Kalmus, 1955) to \(~0.2\%\) (Went & Pronk, 1985).

Rates of congenital CVD vary by broad geographic region due to differing gene pools. Accurate assessments of prevalence require very large sample sizes, and for studies to have unbiased recruitment strategies. As a result, some of the high variability in smaller studies cannot be taken as an accurate reflection of differences in prevalence. The prevalence of any form of CVD is higher in European Caucasian populations (around 8% and 0.4% for men and women respectively) than in Chinese and Japanese
populations (4% - 6.5% of men; Birch, 2012). Smaller studies have identified lower rates of CVD in African populations: 3.60% of men and 0.81% of women (Williams et al., 1998). However, these findings are based on smaller studies in isolated populations, so do not provide conclusive evidence. The gender split in CVD prevalence differs with location, with Asian populations showing a greater proportion of females with CVD (Birch, 2012). The broad survey of prevalence studies examined by Birch (2012) provides evidence that differences in prevalence of CVD by region are due to the genetic drift caused by migration, instigated by the prevalence of CVD among population founders of certain regions, rather than by natural selection.

1.4.6 Perceptual consequences of colour vision deficiency
The common phrase “colour blindness” is a misnomer, as the vast majority of cases retain some discrimination of colour. The reduced range of L/(L+M) signals of the anomalous trichromatic system results in a reduction in sensitivity along that axis, but some ability to discriminate differences in L/(L+M) remains, preserving the three dimensionality of colour vision. The two types of red-green anomalous trichromacy can be distinguished behaviourally by their different effects on colour matching. For a Rayleigh match, the deuteranomalous observer requires more green in the mixture of red and green needed to match a narrowband orange than the average normal trichromatic observer, while the protanomalous observer requires more red (Jägle et al., 2005).

Dichromacy, caused by the absence of an entire cone class, reduces the dimensionality of colour vision to a single axis, comparing the activities of the two remaining classes. This results in a substantial loss of chromatic gamut, with dichromats having only 7% of
the normal trichromat’s number of discernible colours (Linhares et al., 2008b). This lost dimension can be identified in CIE xy space along radial lines describing dichromatic metamers (indiscriminable chromaticities). These lines of indiscriminable colours are not parallel but emanate from a point known as the copunctal point, positioned outside the spectrum locus in a different position for each form of dichromacy (Fry, 1992). The axes along which the ability to discriminate colours is reduced in anomalous trichromacy roughly follow the confusion lines of the corresponding class of dichromacy.

Confusion lines are the logical foundation of many diagnostic tests for CVD, as they identify the sets of chromaticities that are indiscriminable (or less discriminable than in normal trichromacy) for each observer type (Vingrys & King-Smith, 1988). The analysis of errors in tests such as the FM100, involves identifying which set of confusion lines the errors coincide with (Vingrys & King-Smith, 1988). Detection tests and pseudoisochromatic plates use chromaticities along confusion lines to create figure ground segregation tasks expected to be impossible for certain observer types. Diagnostic tests for CVD will be covered in greater detail in Section 1.6.

1.4.7 Functional consequences of colour vision deficiency

The impact of the reduced colour gamut of dichromatic and anomalous trichromatic observers must be judged in a holistic sense as well as a quantitative sense, as colour is critical for visual perception in daily life (Cuthill et al., 2017; Mollon, 1989). Colour aids our awareness of what is around us, informing visual judgements and guiding our attention to important objects or features. Despite the reduction in the number of discriminable colour signals, colour continues to be a valuable source of information for
people with CVD, demonstrated by the role of colour in CVD performance in visual memory tasks (Wichmann et al., 2002), and anomalous observers using colour in visual search tasks even when colour provides limited useful information for the task (Kugler et al., 2015). In daily life, both dichromats and anomalous trichromats report difficulty with aesthetic judgements such as selecting clothes, paints, or cosmetics as the most difficult non-occupational challenge (Cole, 2004). 75% of CVD observers report difficulties with daily tasks, such as cooking meat, selecting ripe fruit, and judging the health of complexions (Collins, 2013). Although normal colour vision is not a requirement to hold a driving licence in the UK, some administrations such as Hong Kong, and, in the past, Australia and Thailand (Cole, 2016) have required no more than 2 errors on the Ishihara Plates test.

Colour vision deficiency can preclude participation in certain occupations where misperception of colour signals carries risk, for example, normal colour vision is typically a requirement for pilots, train drivers and the fire service (Barbur & Rodriguez-Carmona, 2012). Besides industries that individuals with CVD are restricted from, over 100 occupations have been identified in which individuals with CVD are thought to face practical disadvantages (Taylor, 1997). CVD can pose substantial difficulties for individuals in clinical and medical practice, particularly in the identification of blood, skin conditions (Campbell et al., 2004) and pallor (Spalding, 2004), putting patients at risk of delayed treatment and medical error (Goh et al., 2014). The implications of CVD in clinical practice covers a range of tasks from aesthetic judgements in dentistry, such as shade errors in tooth reconstruction (McMaugh, 1977), to symptom recognition, with an increased error rate in reading colour-based test results (Campbell et al., 2000).
In educational contexts, children with CVD may face barriers to learning, with many teaching staff misattributing the difficulties of pupils with CVD as a learning disability, assessing pupils with CVD as poorer achievers (Suero et al., 2005). A significant relationship was found between colour vision deficiency and placement in classes for the “educationally handicapped” among 8- and 11-year-olds in Orange County, USA, which was interpreted as evidence that disruptive behavioural patterns may be associated with failures to cope with the inaccessibility of colour-encoded information in early education (Espinda, 1973). Colorimetric analysis of Catalan maths textbooks revealed that 10% of textbook content required the discrimination of confusion colours for the questions to be answered correctly (Torrents et al., 2011), which could not only be a directly limiting factor in CVD children’s academic achievement but could also be a cause of frustration and disaffection (Espinda, 1973).

1.5 Measuring colour vision
Psychophysics is a scientific tool for measuring percepts created by physical stimuli, by interpreting controlled human behaviour. The key components of a psychophysical experiment are stimulus, task, measure, method, and analysis (Kingdom, 2012). In this section, some common psychophysical approaches will be introduced for the examination of colour vision both at and above threshold in terms of tasks, including the questions posed to the participants, and the overall structure of data collection.

1.5.1 Perception at threshold
A difference threshold is the smallest detectable difference from a stimulus of any intensity, which is distinct from the absolute threshold, which refers to the smallest
stimulus needed for detection at all, for example the smallest amount of colour on an achromatic ground (Kingdom, 2012).

Tasks used to measure discrimination thresholds often fall into the categories of detection or adjustment. Detection tasks such as interval forced choice (IFC) and alternative forced choice (AFC) present a target on a blank surround or amongst a set of non-target ‘distractors’, either separated temporally (IFC) or spatially (AFC). Forced-choice tasks are referred to by their acronym preceded by the number of options presented at each trial (i.e., 2IFC, 4AFC).

A threshold indicates the smallest stimulus needed for a correct detection to occur. Due to the presence of internal and external noise, an observer’s performance does not depend on the intensity of the stimulus alone. Noise fluctuates from trial to trial, meaning there will be no single point at which the signal from the stimulus is reliably greater than the noise. By collecting multiple responses to each level of stimulus and plotting the proportion of correct detections at each stimulus intensity as a psychometric function, it is possible to determine the detection threshold – the stimulus intensity at which a certain proportion of the responses are correct. The following are methods of collecting the responses on which to base the psychometric function. The choice of which approach to use depends on how closely the threshold can be anticipated.

In the method of constant stimuli, trials are presented with stimuli at intensities chosen to straddle the anticipated threshold, where the responses are expected to range from chance in response to subthreshold stimuli, to near 100% correct. With sufficient trials this method produces data that can be fit with a psychometric function, demonstrating
the threshold stimulus intensity required to reach the criterion proportion of correct
detection set by the experimenter.

In situations where there is no anticipated threshold, a staircase method may be a more
appropriate way of choosing trial intensities. This is a form of adaptive procedure in
which the stimulus is altered according to the participants’ responses. Each incorrect
response is followed by an increase in target intensity, each correct response followed by
a reduction in intensity, with a change in response recorded at as a staircase “reversal”. This
procedure can be carried out in either direction; beginning subthreshold and
increasing stimulus intensity monotonically until there is a change in response or
beginning with an easily discriminable stimulus (suprathreshold), reducing the intensity
monotonically until there is a change in participant response. The procedure may be
terminated after a predetermined number of response reversals is met. The detection
threshold can be determined as the average of the stimulus intensities at a specified
number of reversals, or the data can be fitted with a psychometric function (Kingdom,
2012).

Bayesian staircases are an extension of adaptive staircase procedures in which the next
trial in a series is determined as the current best estimate of the threshold, based on
responses to all the previous trials and a prior estimate. Examples of this, such as
QUEST, developed by Watson and Pelli (1983) are very efficient as they calculate the
maximum likelihood estimate of the threshold by fitting a probability density function to
all available data after each trial.

1.5.1.1 Adjustment
The method of adjustment involves the participant adjusting the stimulus itself along a fine-grained scale, until some criterion is met. Adjustment can be used to measure sensitivity as the inaccuracy in matches accepted as identical. For example, for the Rayleigh match, the adjustment is made linearly along one of two dimensions at a time, and the extent of error in both directions describes the observer’s sensitivity. The Rayleigh match is the gold standard in colour vision deficiency diagnosis and will be detailed further in Section 1.6.1.

A foundational use of the adjustment method was MacAdam’s demonstration of the non-uniformity of the CIE 1931 chromaticity diagram (MacAdam, 1942). Measurements were made using the method of adjustment at 25 points in the CIE 1931 chromaticity diagram, whereby observers adjusted one half of a bipartite field until it matched the opposite half. The Macadam colour discrimination ellipses demonstrated a dimension of reduced sensitivity within the CIE 1931 chromaticity space which aligned with the daylight locus and contributed to attempts to construct a perceptually uniform colour space (Bosten et al., 2015).

1.5.2 Methods of measuring suprathreshold perception

Suprathreshold perception refers to all visual judgments of stimuli that have a magnitude substantially greater than threshold, and can include judgements of appearance, intensity and constituent components of appearance (e.g. hue, saturation, lightness).

1.5.2.1 Hue Scaling
Hue scaling is a widely used method for investigating suprathreshold colour perception and can be applied to the question of what opponent response functions underlie percepts of colour. Participants are asked to decompose stimuli into the contributions of each from an array of focal or primary colours. De Valois et al., (1997) found that when asked to indicate the constituent proportions of cardinal colours in stimuli (proportions of red, green, yellow and blue) via colour-coded response buttons, participants preferred to indicate mixtures on a five-point scale over a three point scale (Boynton & Gordon, 1965) but did not require the 100-level scale used by Abramov et al., (1990). When indicating proportions of the 4 cardinal colours using a 5-point scale, observers tended to report no more than 2 hue components at once (de Valois et al., 1997).

1.5.2.2 Maximum Likelihood methods

Maximum likelihood difference scaling (MLDS) and maximum likelihood conjoint measurement (MLCM) are two comparatively new psychophysical methods for investigating suprathreshold perception (Maloney & Joong, 2003; Maloney & Knoblauch, 2020). These methods assign values to the observers’ perception of the stimuli, so that absolute differences between scale values accurately predict observer judgements. In the case of both MLDS and MLCM, two pairs of stimuli are typically presented at once (forming a quadruple) allowing the observer to make a comparative judgement as to which pair shows the greatest difference in the attribute being tested. The data from a few hundred quadruples are used to plot a smooth sigmoidal function, representing the perceived differences along the monotonic scale through which the stimuli varied. This method was recently used by Werner et al., (2020) to investigate changes in chromatic
sensitivity. MLCM is closely related to MLDS but is adapted to allow the contributions of multiple dimensions of stimulus variation to the modelling of behaviour. MLCM has been used to investigate interactions of gloss and surface texture (Ho et al., 2008), surface lightness and gloss (Hansmann-Roth & Mamassian, 2017) and lightness and chroma (Rogers et al., 2016).

1.5.2.3 Colour Matching

As well as being a method of measuring colour discrimination (Section 1.5.1.1), colour matching is a useful approach for measuring colour appearance. Colour Matching experiments contain an adjustment task, using computerised procedures or specially designed devices, in which there is a target stimulus and a test stimulus for the participant to alter until both appear identical. This paradigm can be adjusted to investigate colour constancy by presenting the two the target and test stimuli under separate lighting conditions (Rogers et al., 2020), to test metamerism (Silverstein & Merrifield, 1985), memory effects by presenting the test stimulus and target stimuli at an interval (Pérez-Carpinell et al., 1998) or to measure fine-grained effects on colour appearance, such as the cognitive impact of colour-diagnostic objects on chromaticities accepted as achromatic (Witzel et al., 2018).

1.5.2.4 Multidimensional Scaling

Multidimensional scaling (MDS) is a statistical technique that allows identification of the underlying dimensions giving rise to judgements of similarities or differences within a set of stimuli. It does this by converting numerically described difference ratings into Euclidean distances, resulting in a spatial representation that preserves the relationship
between each item to all other items in the set. Each item in the stimulus set is represented by a point in the MDS solution, which is arbitrary but determined entirely by its relations to all other stimuli. The procedure as described by (Kruskal, 1964) uses only a rank ordering of the similarity or dissimilarity judgements, which means that any linear transformation applied to all values, or translation of values from similarity to dissimilarity ratings will have no impact on the solution.

Shepard’s modification of the method (Shepard, 1962) introduced a monotone relationship between the pairwise difference ratings and the pairwise stimulus distances in the solution. In this way the solution must preserve the order of the distances between the stimuli in the difference judgements. Later, Kruskal (1964) added a measure of the quality of a solution, referred to as the stress, calculated from the residual variance in the regression between the difference ratings and distances in the solution. As a residual sum of squares measure, the less stress in an MDS solution, the better the solution.

The MDS input data is usually a matrix of pairwise ratings of the differences between all stimuli in a given set, including a baseline of zero for stimuli paired with themselves. Interval or ratio level data requires a metric MDS procedure and ordinal data requires a non-metric procedure (Shepard, 1962). When using MDS to examine visual perception, a linear relationship cannot usually be assumed between the physical differences between stimuli and the perceived differences, and therefore a non-metric MDS procedure is usually preferred (Jordan et al., 2010).

The number of dimensions in an MDS solution is unconstrained; formally and mathematically it is possible for a solution to have any number of dimensions, although
the appropriate number of dimensions is a matter of scientific judgement that can be
guided by the rate of reduction in stress as dimensions are added (Kruskal, 1964), or
Bayesian approaches can be used (M. D. Lee, 2001). The dimension with the greatest
variance appears as the first dimension. As the information within an MDS solution is
in the relationship between the points, analyses such as Procrustes allows for the
transformation, via rotation or reflection of the entire solution, without undermining its
integrity. This enables interpretation, and in the case of coloured stimuli, permits
alignment of a solution with the axes of a colour space. A detailed investigation of the
robustness of multidimensional scaled solutions after Procrustes analysis is presented by
(Sibson, 1978).

MDS has often been used to measure colour appearance, and several studies have used
it to investigate colour perception in CVD. For example, Bosten et al., (2005) used MDS
to identify a dimension of colour that is discriminable to deuteranomalous observers but
not to normal trichromats. Two sets of stimuli were produced using single pigment
paints, one set consisting of mixtures of cobalt blue and cadmium yellow, the second set
consisting of varying proportions of yellow oxide and ultramarine blue. Two-dimensional
MDS solutions showed a clear segregation between stimulus groups in the dissimilarity
ratings given by deuteranomalous observers, but no separation between the groups in
the normal trichromats’ solutions. Later research used MDS to investigate the possibility
that some carriers of deuteranomaly gain tetrachromatic vision by using the anomalous
cone class present alongside the three normal trichromatic cone classes in the retina.
The same two sets of stimuli (as used in Bosten et al., 2005) were presented to the
mothers of deuteranomalous observers. Most carriers were not able to distinguish the
two sets of stimuli, but one carrier was able, suggesting that they possessed functional
tetrachromacy (Jordan et al., 2010). Boehm et al., (2014) used Procrustes analysis to
rotate MDS solutions to realign the points with the axes in the physiologically relevant
MacLeod Boynton chromaticity diagram. Doing this allowed them to measure differences
between normal trichromats and anomalous trichromats in suprathreshold perception by
comparing the dimensions of the MDS solutions aligned with the cardinal axes.

1.6 Identifying CVD
A great many tests have been developed to identify CVD. The following section will
introduce the most common tests in three categories: matching tests, arrangement tests
and pseudoisochromatic tests. The principles that guide each form of test will be
examined, with commonly used examples of each type of test introduced, followed by an
assessment of the strengths and weaknesses of each approach.

1.6.1 Matching tests
Matching tests identify CVD according to the proportions of two narrow-band lights
required to match a third narrow-band light. The most commonly used matching test
for identifying x-linked CVD is the Rayleigh match, in which proportions of red (670
nm) and green (545 nm) lights are adjusted until they match the appearance of a yellow
(589 nm) light (Pokorny et al., 1982). The proportions of red and green in the accepted
match reveal the observer’s sensitivity to red and green, allowing inference of their colour
vision phenotype (Sanocki et al., 1997).

The anomaloscope uses the Rayleigh match to identify X-linked CVDs. The less common
Engelking Trendelenburg match, and the Pickford-Lakowski match are implemented in
devices designed to identify tritan deficiencies (Pokorny et al., 1982). A small range of commercial anomaloscopes are available including the Nagel (Schmidt and Haensch, Berlin, Germany) the Okulus (Wetzlar, Germany), and Neitz (Tokyo, Japan) which deploy the Rayleigh match, and the Pickford-Nicholson (Rayner and Keiller, Ltd., London, England) which deploys the Rayleigh match as well as the Engelking Trendelenburg match and the Pickford-Lakowski match (Pokorny et al., 1982). Standard clinical devices use monochromatic wavelengths ~589 nm (sodium yellow), ~545 nm (mercury green) and ~670 nm (lithium red) as the primaries for the Rayleigh match. Research focused on colour vision deficiencies has also been carried out using custom anomaloscopes (Trukša et al., 2012) using multiple optical channels to present a narrowband test stimulus and adjustable matching stimuli (Boehm et al., 2014; Shevell & He, 1997). The Rayleigh matching task requires the observer to adjust the proportions of red and green lights contributing to one half of a stimulus field to match a chromatically fixed half comprising monochromatic yellow. The brightness of the matching yellow is adjustable, to allow observers with different luminosity functions to make perfect matches, including protan observers who receive a lower luminance contribution from the red stimulus.

The scoring differs for different anomaloscopes, with each device assigning differing values to the mixing primaries. In the case of the Nagel anomaloscope the mean ratio of green to red in accepted matches are recorded as the Anomaly Quotient (AQ) and is represented in the Pitt diagram (Oculus, 2015), which plots the red-green proportion of matches along the abscissa, and the luminance setting of the matching yellow up the ordinate. During the test each match is recorded, and both the midpoint and matching
range are used as descriptors of the observer’s CVD type and severity (Pokorny et al., 1982). Deuteranomalous observers are less sensitive in the green portion of the spectrum and so require a higher proportion of green in the mixture to make a match (AQ 1.4 to 20). Protanomalous observers are not only less sensitive to red, but in severe cases, have a shorter visible spectrum, and so not only require more red in their chromatic mixture (AQ 0.7 to 0.1), but to also reduce the luminance of the yellow matching stimulus in order to make a match. Extreme anomalous trichromats are typified by wide ranges in their accepted matches, accepting mixtures within the normal range as well as the deuteranomalous or protanomalous range, but rejecting mixtures comprising only one of the primaries (AQ of $\infty$ and 0 not accepted as matches). Dichromats are unable to discriminate the difference between the red and green components of the mixture, and so accept matches throughout the adjustable range, (AQ extending to $\infty$ and 0 respectively).

This anomaloscope is specific enough to be able to discriminate between classes of CVD, with distinct results from all classes of anomalous trichromat, extreme anomalous trichromat and dichromat. It is considered the gold standard for detecting colour vision abnormalities (Birch, 2012), and as such, the sensitivity and specificity of other tests for CVD are calculated in comparison to the outcome of anomaloscope tests (Pokorny et al., 1982). The correct deployment of the test requires some training (Pokorny et al., 1982), and the test must be used under stable conditions as fluctuations in temperature and power supply have been found to influence its function (Jägle et al., 2005).
The Pickford Nicholson anomaloscope has some advantage for testing those with restricted verbal communication, such as the young, non-fluent or learning disabled, as it allows both the examiner and the test subject to point to the hemispheres rather than describe what is seen (Lloyd et al., 1984).

1.6.2 Arrangement tests
Arrangement tasks identify CVD according to the errors made when sorting colours into a sequence. Colours of fixed brightness and lightness, varying only in hue, are used to restrict the information available to that which is diagnostically useful. CVD can be identified both by the number of errors made and the classification of the errors according to coincidence with confusion lines.

Arrangement tests, sometimes referred to as panel tests, vary in the number of test colours, the hue difference between test colours, and the saturation of the test colour set. The Farnsworth Munsell 100 Hue test (FM100) is the largest of such tests featuring 85 test surfaces, whereas the Farnsworth (Dichotomous) D-15 and Lanthony (Desaturated) D-15 feature 15 test surfaces. The FM100 is presented in 4 separate sections to restrict errors to neighbouring regions, rather than between opposite extremes of the colour circle. Errors are interpreted by coincidence with portions of the colour circle that run along a confusion line. Each section comprises 21 or 22 coloured caps featuring colour differences small enough that normal observers are expected to make some errors.
The Farnsworth (Dichotomous) D-15 test (Farnsworth, 1943a) is an abridged version of the FM-100, in which errors made between neighbouring chips are not interpreted as indicative of CVD, but instances of errors that cross the colour circle (or dichotomise it), are. The class of CVD, protan, deutan or tritan, is indicated by errors aligning with the relevant confusion line. The test does not definitively separate mild CVD from moderate CVD, but a result including 10 or more errors is considered to indicate severe CVD (Good-lite, Elgin Illinois USA). An inconclusive result in the Farnsworth (Dichotomous) D-15 can be clarified using the Lanthony (Desaturated) D-15 test (Lanthony, 1978). This test is similar to the Farnsworth D-15, using Munsell surfaces with the same hues as the Farnsworth D-15 but of lower saturation (chroma) and luminance (value) to make the test harder, and better separate normal observers from those with a mild or moderate CVD. The scoring procedure is identical to that of the Farnsworth D-15, identifying CVD by errors which cross the colour circle aligned with a certain confusion line (Good-lite, Elgin Illinois USA).

The FM100 is a fine-grained measure of colour vision, enabling the identification of acquired colour vision deficiencies as well as protan, deutan and tritan deficiencies (Pokorny et al., 1982). Due to the high saturation of the test stimuli, the Farnsworth D-15 has limited effectiveness in discriminating mild anomalous trichromats from normal trichromatic observers, but when combined with the less saturated Lanthony D-15, the combined results are capable of identifying mild degrees of discrimination loss (Lanthony, 1978). Considerable within-subject variability has been found when assessing the reliability of the Lanthony D-15, with at least three administrations required to reach clinical standards of reliability (Good et al., 2005).
Tests for colour vision deficiencies which use physical surfaces are vulnerable to the impact of the lighting used. Manufacturers of the FM-100 tests suggest CIE Standard Illuminant C as the ideal illuminant, as the tests are known to be weakened by tungsten illuminants, under which deutan observers make fewer errors and protan errors align with the deutan confusion axis, resulting in misdiagnoses (Higgins et al., 1978). The scoring of arrangement tests usually requires plotting the individual confusions on a polar diagram before they can be interpreted, meaning these tests have a greater training requirement than others such as plates tests.

1.6.3 Pseudoisochromatic tests
‘Pseudoisochromatic’ refers to representations in which a target is rendered using chromaticities intended to be visible for normal trichromatic observers but indistinguishable for observers with CVD (Birch, 2010). Pseudoisochromatic plates are designed to offer no information about the target aside from the chromatic difference from the background. The form of the target is disguised by both the target and ground consisting of a fragmented pattern, with any observer-specific luminance signals in the chromaticities of the target disguised by greater luminance variation equally distributed across both target and ground. Pseudoisochromatic designs can be combined with identification or detection tasks, and in some cases diagnoses of the type of CVD can be made according to the confusion axes the plates’ chromaticities fall along.

Physical plates tests employ the pseudoisochromatic principle to present targets defined by chromaticities that differ from the ground chromaticities along the confusion axes of different colour vision phenotypes. The Ishihara plates test includes the greatest variety of plate designs, with “vanishing”, “transformation”, “hidden digit” and “diagnostic”
plates. The “vanishing” design features targets defined by chromatic variation along a confusion axis. The “transformation” design presents a digit with a vanishing portion, so that different observer types identify different digits. The “hidden digit” design features a target defined by luminance variation instead of hue variation, intended to be more discriminable to those with CVD, with the luminance information of the target masked by chromatic noise visible to those with normal trichromacy. “Vanishing”, “transformation” and “hidden digit” plates are designed to be screening tools to identify the presence of any CVD, but not the type or severity. The Ishihara test includes four “diagnostic” plates which provide some indication of the type of deficiency, by featuring two targets, one defined by deutan confusion colours and the other by protan confusion colours. The Hardy Rand Rittler test (HRR; Hardy et al., 1954) is a physical plates test featuring “diagnostic” plates which present separate deutan and protan targets within each plate. The Neitz and Neitz test, (M. Neitz & Neitz, 2001) presents shapes within “vanishing” designs, which also feature a distractor defined by luminance rather than hue difference, with responses given as a 4AFC multiple choice. The City University test (2nd Ed, London, UK) applies the pseudoisochromatic principle to a matching task, in which the observer must identify the matching colour from for dots surrounding the test dot, with the potential matches including chromaticities selected along protan and deutan confusion axes as well as a colorimetric match.

Computerised colour vision tests replicating the physical plates tests have been developed, but in order for digital tests to be effective they must be presented on calibrated monitors, limiting their viability for testing for CVD remotely. The flexibility of digital presentation has been used to extend the testing paradigm to create more
rigorous tests of chromatic sensitivity. The Colour Assessment and Diagnosis (CAD) test determines chromatic sensitivity by asking observers to indicate when a coloured target is visible, while the target varies by hue, saturation and location on an achromatic ground featuring dynamic luminance noise (Barbur, 2004; Barbur & Rodriguez-Carmona, 2017). The test quantifies the extent to which colour sensitivity at threshold is reduced compared to the normal trichromat in Standard Normal CAD units (SN). Anomalous trichromatic observers are expected to have thresholds greater than 1 SN for \( L/(L+M) \) colour differences, but normal thresholds for \( S/(L+M) \). Deuteranomals produce SNs for the \( L/(L+M) \) axis between 2.79 and 22.44, whereas protanomals show thresholds ranging from 4 to 12.67 SN (Barbur & Rodriguez-Carmona, 2017).

The Cambridge Colour Test presents a four alternative forced choice task in the form of a Landolt-C, in which the observer must identify the location of the break in a circle varying from the achromatic ground along a certain colour axis (Regan et al., 1993). The test measures colour detection thresholds along 20 hue angles in CIE \( LUv' \) space, used to plot discrimination ellipses. These ellipses can be used to describe the extent of CVD by comparing the ratio of the longest axis, oriented along the respective confusion axes where colour discrimination is worst, to the shortest axis, representing the colour direction with the greatest sensitivity. Dichromatic observers typically produce ellipses with axis ratios of over 12 (Regan et al., 1993). Anomalous trichromatic discrimination ellipses vary greatly, with observers with the mildest forms of anomalous trichromacy giving axis ratios close to those from normal trichromatic observers, to extreme anomalous trichromats showing axis ratios greater than some dichromats (Regan et al., 1993). The CAD test has been found to have 98% specificity in screening for CVD in
comparison to the Nagel anomaloscope (Rodriguez-Carmona et al., 2005). The Cambridge Colour test and the CAD test are able to measure fine-grained information about observers’ sensitivities to colour allowing differentiation of protan, deutan and tritan classes of dichromacy and anomalous trichromacy, according to the elongation and angle of discrimination ellipses (Regan et al., 1993).

Although the Ishihara Plates test has very high sensitivity and specificity as a screening tool, differentiating CVD observers from normal trichromatic observers, it is less effective at differentiating specific types of CVD (Pokorny et al., 1982). The sensitivity varies across plate designs, with the “transformation” and “vanishing” plates showing a combined sensitivity of 99% with three errors, but “hidden digit” plates showing a sensitivity of less than 50% (Birch, 1997b). The HRR test also shows high sensitivity (1.0) and specificity (0.96) for screening purposes (Birch, 1997a). Despite limited ability to assign phenotypes, the HRR and Neitz and Neitz tests give some indication by rating observer responses according to deutan and protan categories, with three levels of severity.

The sensitivity of the Ishihara Plates test varies according to the fail criterion used, with a sensitivity of 98.4% with three errors, reducing to 97.7 and 94.7% when the fail criterion is increased to 4 and 5 respectively (Birch, 2010). Normal trichromats have been found to make up to 6 errors on the Ishihara plates test (Birch, 1997b), in part due to the serifed typeface of the targets (Cosstick et al., 2005; Miyahara, 2008), meaning there is considerable overlap between the performance of normal trichromats and the standard 3-error fail criterion (Birch, 2010). The HRR test has its greatest screening sensitivity
when the fail criterion is 2 errors (92.8%), reducing to 87% with a fail criterion of 3 errors (Birch, 2010). Despite a sensitivity of 1.0, the Neitz and Neitz test has been found to have a specificity of 86.4%, suggesting a high false-positive rate (Block et al., 2004; Tang et al., 2022). There is a trade-off between sensitivity and specificity, with a more liberal criterion for CVD providing higher sensitivity but lower specificity. Physical plates tests, such as the Ishihara Plates test, the Neitz and Neitz test and the HRR test have the advantage of being relatively low cost, portable and easy to administer. But despite being generally reliable (Birch, 1997b) the test results can be misinterpreted due to the sensitivity of the tests being highly dependent on the pass criteria used.

1.7 Modelling colour vision
Mathematical modelling is the practise of creating a mathematical representation of a process. The accuracy of a model of colour vision depends on how precisely the factors involved in colour vision are estimated. With modelling it is possible to predict colour discrimination, colour appearance, and changes in sensitivity due to adaptation (Clifford et al., 2007). It is possible to model the chromatic sensitivity of any observer type: observers with CVD can be modelled distinctly from normal trichromatic observers. The stages of a model of the colour signals available to specific observers can be summarised as the external input (Figure 2, 1-2), receptor responses (3-4), and the signals available at early stages of processing (5-6).
Figure 2. The radiance of light reaching the eye is comprised of the SPD of the illuminant (2), attenuated by the reflectance of any surfaces it interacts with (2). The cone activity in response to this radiance can be calculated using the cone fundamentals of any given observer (3), which determine the activity in response to the energy at any given wavelength (4). These activations can be summed across wavelengths to give the total activity of each cone class (5). Retinogeniculate cone-opponent signal can then be estimated as the MacLeod Boynton chromaticity coordinates: $S/(L+M)$ and $L/(L+M)$ (6).

1.7.1 Modelling external input

All external light reaches the eye as radiances, combining the light from an illuminant with that reflected from the surface being observed. It is possible to separate the radiance spectrum of an illuminant from the reflectance spectrum of a surface by measuring the SPD of a known surface under the illuminant. This is commonly done using a standard white surface, specially designed to reflect equally at all wavelengths. The measurement of this surface indicates the radiance at each wavelength of the illuminant, which can be separated from further measurements of other surfaces under the same illuminant.

This model provides an approximation of spectral visual input for a particular point on a particular surface, but a more complete model of visual inputs could make use of recent...
advances in hyperspectral imaging, which record SPDs for every pixel in a scene. The development of hyperspectral imaging has allowed calculation of the constriction of chromatic information conferred by CVD (Linhares et al., 2008b), the response of the visual system to specific visual diets.

1.7.2 Modelling receptor activities
To create a model of the colour information available to particular observers, it is necessary to standardise a certain amount of natural variation found within each observer type. Section 1.4 presented the diversity in spectral sensitivity to light in normal trichromatic observers (Section 1.4.4) and in observers with different categories of CVD (Section 1.4.2).

Cone fundamentals obtained in vivo using psychophysical measurements provide sensitivity information in the context of all the living tissue of the eye, characterising the cone sensitivities in response to radiances which includes the effect of filtering by ocular material. In vivo cone fundamentals can be found through direct methods such as densitometry, micro-spectrophotometry and suction electrode recordings (Stockman et al., 2000). Technical innovations have made it possible to measure the spectral sensitivities of individual cone classes (Baylor et al., 1987; Dartnall et al., 1983; T. W. Kraft et al., 1998) and to directly measure the effect of amino acid sequence differences on spectral sensitivity (Merbs & Nathans, 1992a, 1992b). Psychophysical methods based on colour matching have been found to estimate cone sensitivity functions more accurately than direct methods based on imaging and are best derived from dichromats
genotyped to ensure that the cones involved are identical to those possessed by normal trichromats (Smith & Pokorny, 1975).

Dichromatic colour vision can be modelled as a reduced form of normal trichromatic vision by the removal of one cone class. A model of protanopia includes S and M cone classes, deuteranopia S and L cone classes, and tritanopia M and L cone classes. A model of anomalous trichromacy requires anomalous cone fundamentals. A ‘standard’ set has been produced by DeMarco et al., (1992), and in-vitro absorption spectra of anomalous cone classes have been identified by photobleaching difference absorption spectroscopy (Merbs & Nathans, 1992b). The nomenclature for anomalous cone sensitivity functions differs. Some sets of fundamentals referring to the cone that has been replaced with an added prime (’), for example, DeMarco et al., (1992) labels the protanomalous cones as S M and L’. Others refer to the anomalous cone in terms of the normal trichromatic cone it most closely resembles, for example labelling the protanomalous cones as S M and M’. In the current work I follow the latter convention. As an alternative to the standard DeMarco et al. (1992) tabulations, various ‘nomogram’ templates allow the generation of anomalous cone classes with any peak spectral sensitivity in conjunction with any macular pigment density and lens density (Stockman & Sharpe, 2000).

Variation in the proportions of different cone classes present in the retina may be represented by scaling the sensitivity functions for cone classes, with the combined L and M classes equalling 1, to represent their combined input to the luminance system. The relative scaling applied to L and M provide a model of how much each cone type inputs to the luminance channel. When modelling a specific individual’s sensitivity with
the intention of presenting controlled stimuli to that observer, it is possible to estimate proportions of cone classes by performing heterochromatic flicker photometry (B. Lee et al., 1988). Here a stimulus alternating between two chromaticities, appears to flicker, flash, or move least at the point of isoluminance. The values of the stimulus identified as isoluminant provide the relative scaling of the L and M cone classes.

The first stage of vision can be modelled by multiplying the spectral power distribution (SPD) of the illuminant by the SPD of the surface being observed, to gain the radiance entering the eye, which is then multiplied by the sensitivity functions of each cone class and summed over wavelengths to give the cone class’s predicted activity.

1.7.3 Modelling retinogeniculate colour representation

The previous steps detail how to model cone activities of defined observers in response to spectrally characterised stimuli. To extend the model beyond receptoral activities to represent the activities of retinogeniculate colour opponent mechanisms, representations of the three ‘cardinal’ channels must be calculated. The model used by Jordan et al., (2010) and Moreland et al., (2010) estimates signals available in the opponent channels as \( \frac{L}{L+M} \) for chromatically opponent midget ganglion cells, \( \frac{S}{L+M} \) for small bistratified ganglion cells, and \( L+M \) for the luminance signals carried by midget and parasol cells.

Models representing chromatic adaptation have taken a similar physiologically accurate approach to Jordan et al., (2010) and Moreland et al., (2010) but have extended them to represent a state of complete adaptation by “centring” signals according to the mean of a reference input for each cone class, known as Von Kries adaptation (von Kries, 1970).
In the case of chromatic adaption to differing scenes, L, M and S activations were scaled to the mean in response to a reference scene (Juricevic & Webster, 2009). A model of chromatic adaptation within anomalous trichromatic observers used this approach, but rather than a reference scene, the means of cardinal signals were equated between anomalous trichromatic observers and the equivalent cardinal channels of a standard normal trichromatic observer (Webster et al., 2011) using a multiplicative transformation. This approach also allowed the modelling of post-receptoral compensation applied to the attenuated chromatic signals available to anomalous trichromatic observers.

1.7.4 Simulating dichromacy
A simulation is itself a representation, which takes the output from models of visual perception, and represents the reduction in signal diversity or intensity, for the normal trichromatic observer. This form of demonstration aims to not only give a representation of the impact of CVD over the entire colour gamut, but also allows normal trichromatic observers to identify specific instances of information loss. Coblis (Wickline, Human-Computer Interaction Resource Network, 2001) and Vischeck (http://www.vischeck.com, 2012) are online algorithms that simulate the CVD appearance for CVD observers by altering digital images. Variantor (Cambridge Research Systems Ltd., Rochester, UK) is a wearable device which uses broadband optical filters to reduce normal trichromatic colour discrimination to a level similar to that of a dichromat.

Vischeck is based on the approach used by Brettel et al. (1997), projecting normal trichromatic colour differences onto an equivalent dichromatic plane. This translates the absence of a cone class into the a* b* values of a version of CIE L*a*b* space (Bäuml &
Wandell, 1996; Zhang & Wandell, 1997). The values used in this process were validated using matches made by unilateral dichromats (Judd, 1949), observers with one trichromatic and one dichromatic eye. The authors acknowledge that little is known about the genetic basis of unilateral dichromacy, and that the cone sensitivities of the normal trichromatic eye of a unilateral dichromat may not resemble the cone sensitivities of a normal trichromat.

1.7.5 Simulating anomalous trichromacy
To simulate the visual experience of anomalous trichromats for normal trichromats, the reduction in sensitivity to colour contrast in anomalous trichromacy is applied to reduce chromatic diversity for normal trichromats.

Lucassen and Alferdinck (2006) presented a model designed specifically for the simulation of anomalous vision for the normal trichromatic observer. The model estimates the quantal catches of anomalous cone classes using a linear combination of the normal trichromatic L and M cone activities, with the proportions of L and M in the combination weighted according to the “degree” of anomalous trichromacy. The estimated anomalous cone activities are transformed to RGB to display the simulation. Note that this approach may produce reasonably accurate simulations for RGB images but because intermediate cone fundamentals are not actually modelled, they do not accurately model anomalous trichromatic colour signals in response to arbitrary spectra.

Webster et al. (2011) created a model of anomalous cone fundamentals by translating normal L and M cone fundamentals 6nm along the wavelength axis. In their simulations of anomalous trichromacy they included a model of impact of postreceptoral compensation on the chromatic signals available to anomalous trichromats (Webster et
al., 2011). Following scaling of each cone’s mean response to model von Kries adaptation, they modelled contrast adaptation by scaling the range chromaticities along each anomalous cardinal colour axis so that it matches the range for the equivalent channels for a standard normal trichromatic observer. In order to simulate how these processes affect perceived colour, chromaticities are converted first to LMS values and then to RGB values for display.

1.8 Interventions for CVD
The following section will discuss the methods that have been used to alleviate the effects of colour vision deficiency, from genetic treatments which offer the most permanent solution but the greatest cost, to the low-commitment solutions of aids that alter visual information, to optical filters which attempt to alter the spectral content of light reaching the eye in order to enhance colour discrimination.

1.8.1 Genetic treatments
Functional colour vision requires both multiple receptor types and appropriate neural wiring to process receptor signals. Colour vision deficiencies are caused by either missing or weakened responses from receptors. The viability of genetic treatments for CVD to restore receptor function depends on whether the neural circuitry needed to process normal trichromatic colour vision signals is intact in individuals with CVD. This has been investigated in mammalian and primate visual systems. The retinas of most non-primate mammals have two cone classes, supporting dichromatic colour vision. Old world and some new world primates possess the genes for a third cone photopigment, which
in some species is only expressed in the retinae of heterozygous females, but in others is expressed in both sexes (Jacobs, 1998).

The primate visual system has parvocellular pathways, magnocellular pathways (B. Lee, 1996) and koniocellular pathways (Hendry & Reid, 2000), much like the human visual system, and it has been suggested that the midget bipolar and ganglion cell systems are sufficient that only the addition of a new photoreceptor is required for dichromatic primates to process trichromatic colour signals (Mollon, 1989; Wässle, 2004; Wässle & Boycott, 1999). The potential for genetic engineering to thus bestow dichromatic colour vision systems with trichromatic colour vision has been tested by engineering knock-in mice expressing the human L cone photopigment in addition to their native M photopigment (Jacobs et al., 2007). Of seven heterozygous knock-in mice, three demonstrated reduced thresholds in the spectral region of the knock-in L cone sensitivity function suggesting that the knock-in gene had conferred an increase in chromatic sensitivity. Similar results have been achieved using a viral vector-based gene therapy in adult squirrel monkeys (Kuchenbecker et al., 2014; Mancuso et al., 2010). Two dichromatic squirrel monkeys were trained on an animal version of the Cambridge Color Test (Mancuso et al., 2006), establishing an inability to discriminate colours from grey along dichromatic confusion axes, before being given subretinal viral vector injections containing L cone photopigment opsin gene. After 20 weeks both monkeys showed significant improvement in colour detection thresholds.

Gene therapy provides the only current possibility for a ‘cure’ for CVD, and studies employing gene therapy for colour vision in dichromatic animals have so far shown
promising results. The effectiveness of genetic treatments for congenital CVD in visual systems very similar to those of humans have powerful implications as it demonstrates that the neural circuitry used in processing colour signals is able to function normally after a lifetime of privation. Studies trialling this method in humans are planned, however, gene therapy is considered high-risk as the vision of individuals with CVD is otherwise good (Dolgin, 2009).

1.8.2 Screen-based accessibility aids
Visual information viewed on screens can be made more accessible to those with CVD using software that alters chromatic content before it is displayed. The following section will describe the main strategies these interventions use, from point-correction of selected chromaticities, alteration of entire scenes to increase the chromatic diversity for CVD observers, to attempts to retain naturalistic appearance while improving discriminability.

1.8.2.1 Aids to enhance accessibility of colour information
Strategies that focus on transforming colour information aim to limit problems with accessibility of information caused by CVD, rather than to improve or expand colour vision itself. The most basic form of accessibility software aims to reduce the amount of information lost by altering any confusion colours identified within a scene. This form of software is publicly available as apps and browser extensions, such as ColorEnhancer (Google, Mountain View, California, 2016) which improves the accessibility of colours in static website content for CVD observers, and online tools such as Daltonize (Vischeck, https://www.vischeck.com/daltonize, 2012 Vischeck), which adapts individual
images. Built-in accessibility options are becoming more widespread, promoted by guidelines from the Web Content Accessibility Working Group (www.w3.org). There are instances of digital media produced with inbuilt colour accessibility options, such as CVD-appropriate colour options for multiplayer games (Overwatch, Blizzard Entertainment, 2016), for sports games (EA Sports, Redwood City, USA) or with coloured overlays aimed at assisting visual search (Infinity Ward, Encino, USA). Though these technologies are still in their relative infancy and are not yet widespread (Chaparro & Chaparro, 2017), technical advances allowing the enhancement of live video imagery are expanding opportunities for accessibility provisions.

A number of Google Glass (X Development LLC, Mountain View, California, USA) applications have been developed to deliver dis-ambiguating information overlaying the view through the Google Glass. Chroma (Tanuwidjaja et al., 2014) for Google Glass applies a more dynamic approach to colour accessibility using augmented reality. This approach overlays any instance of a preselected colour in the observer’s line of sight with opaque white, enhancing colour-based identification and visual search and allowing a CVD observer to use the device to break a metamerisms. Colorizer (Popleteev et al., 2015) developed software for similar smart glasses, deploying both a selective overlay approach, as with Chroma, and a total gamut alteration approach, increasing the saturation of confusion colours in the line of sight. The gamut shifting approach was deemed less successful in this software than selective colour-identify and replace method (Popleteev et al., 2015), but other attempts at a gamut shifting aids are discussed in the next section.
1.8.2.2 Gamut shifting aids

Another family of accessibility software aims to redistribute the gamut to within the visible range of the CVD observers. Daltonize (Vischeck, https://www.vischeck.com/daltonize, 2012) is the only online simulation tool designed to alter static images which has published research underpinning its function (Brettel et al., 1997), which replaces confusion colours with distinguishable chromaticities by enhancing the chromatic variation along the blue-yellow axis in addition to luminance variation. The strength of this approach is in its ability to introduce visual diversity to confusion colours while retaining somewhat naturalistic appearances of the objects shown, though its validity has not been tested.

Another deployment of this approach is the Self Organising Map algorithm (Ma et al., 2009) builds a non-linear colour map to translate the original colour differences into differences within the two-dimensional dichromatic colour space. This method preserves spatial information, improving discrimination while avoiding confusion colours. Its effectiveness was established by modelling the chromatic diversity of scenes (Pointer & Attridge, 1998). Out of 120 images processed, the average chromatic diversity for protanope before the enhancement was 35.24% of normal trichromats', and after enhancement was 73.42% (Ma et al., 2009). The Self Organising Map or similar algorithms may increase the discriminability of objects depicted and have been shown to break the metamerism of the Ishihara Plates test for CVD observers (Melillo et al., 2017). However, this approach disrupts object colours, reducing recognition, and despite
reducing the number of metamers, does not confer a functional improvement in colour vision.

1.8.2.3 Naturalistic gamut aids

A key limitation all of the methods of enhancement discussed so far is that the colour transformations involve changing familiar object colour contingencies (Connah et al., 2014). Although discrimination between colours may be improved, useful information about object identity may be lost, as well as producing false-colour visualisations which can be difficult to interpret (Connah et al., 2014). To address these limitations of existing algorithms, Finlayson and colleagues have developed a novel technique of ‘image fusion’, using the edge-detection information contained in near infra-red images to adjust the RGB content of digital images, enhancing the clarity of the images for both normal trichromats and people with CVD, while retaining naturalistic colouring (Connah et al., 2014).

1.8.3 Filter-based aids

Filters have been developed with the aim of addressing CVD, deploying a range of approaches to meet different functional goals. Some have been designed to break metamerisms by introducing luminance differences between percepts that would have been identical, and others aim to enhance colour perception by increasing the chromatic information available to the visual system.

1.8.3.1 Interocular filters
Interocular filters break metamerism by differentially filtering each eye with the aim of introducing binocular luminance signals, sometimes referred to as *binocular lustre* (Wendt & Faul, 2022), to break metamers (Sheedy & Stocker, 1984). Variations on this process have been developed by Harris (Chromagen, Birkenhead, United Kingdom; Harris 1996), Zeltzer (X-Chrom, Ipswich, Massachusetts USA; Zeltzer 1971) and without scientific publication by Azman (Colormax, Birmingham, Alabama USA; Muttaqin 2011). These glasses function for both dichromats and anomalous trichromats, as the observer learns to use inter-ocular luminance differences to distinguish confusion colours. A “trial and error” process is used to select a particular filter for a given individual (Harris, 1996), selected to maximise binocular lustre (Hodd, 1998).

Research testing the effectiveness of interocularly-discrepant filters has found that the lustre effect is useful for breaking the metamerism of pseudoisochromatic plates, such as the Ishihara plates test (Oriowo & Alotaibi, 2011; Paulson, 1980; Swarbrick et al., 2001; Welsh et al., 1978), and the Hardy Rand Rittler (Paulson, 1980; Welsh et al., 1978). However, the lustre effect does not enhance sensitivity to colour itself, and thus does not result in improvement in arrangement-type tests such as the FM100 (Kassar et al., 1984; Matsumoto et al., 1983), the D-15 Panel test (Paulson, 1980; Swarbrick et al., 2001) or the Lantern test (Kassar et al., 1984; Paulson, 1980; Swarbrick et al., 2001).

1.8.3.2 Bandpass filters

Binocular bandpass filters are intended to increase the chromatic signals available to anomalous trichromats and are best understood by considering the effect of the filters on the sensitivities of the cones, rather than by considering the attenuation of the light
entering the eye. The pass region of the bandpass filter is positioned in order that the filter differentially attenuates one half of the Gaussian L and M cone sensitivities, with the intention of altering the wavelength of peak sensitivity of the anomalous cone class (Ábrahám, 2001). The earliest range of bandpass filters with the aim of alleviating CVD were developed by Abrahams and Wenzel (Colorlite, previously Coloryte, Budapest, Hungary; Abraham et al., 1995). The method deployed in Colorite products was to construct layers of interference filter designed to selectively alter the peak sensitivities of selected cone classes by attenuating bands of wavelengths; altering the 550 to 780 nm band to address the L cone sensitivity, 580 to 55 nm to address the M cone class, and 380 to 480 nm to address the S cone class. Individual interference filters were tested by combining multiple pre-made layers before a final wearable product was produced.

The effectiveness of interocular (ChromaGen, X-Chrom and Colormax) and binocular filters (Colorlite) have been examined via a modelling approach (Moreland et al., 2010) to estimate the impacts of the filters on the saturations of a large gamut of chromaticities, and on the luminance attenuation of traffic signals. Anomalous observers were simulated using DeMarco et al. cone fundamentals (DeMarco et al., 1992) used to model responses to 16 D-15 Panel test colours, 658 Munsell surfaces, and the red, yellow and green traffic signals specified by the European standard (CEN, 2007). They defined a criterion for “useful colour enhancement” as twice the discrimination threshold for that colour. The results demonstrated that all the filters in question failed to provide useful enhancement for either deuteranomalous or protanomalous observers, and in addition to this attenuated traffic signals to below the level required by the European standard (CEN, 2007).
1.8.3.3 Notch filters

Notch filters have been developed with the same intent as the bandpass filters discussed in the previous section, to selectively attenuate the sensitivities of the L and M type cones present in the anomalous trichromatic retina. The key difference is the selectivity of the wavelengths attenuated by the filter. Notch filters feature multiple spectral regions of high and low attenuation, as opposed to the single region of high and single region of low attenuation in the bandpass design. The potential for notch filters to be used to ameliorate the effect of anomalous trichromacy is based on the premise of selectively attenuating the region of the spectrum where the sensitivities of the anomalous and spectrally neighbouring cones are the most similar. By reducing light at this part of the spectrum, the signals from the two cones are effectively made more different. In this way the filter aims to simulate a greater spectral difference between the peaks in sensitivity of the anomalous and spectrally neighbouring cones. Due to the method of operation, notch filters are not expected to be effective for dichromacy.

The notion of trading luminance for colour signals has been tested through a variety of modelling investigations. The chromatic diversity of natural scenes has been found to increase for normal trichromatic observers when viewed in conjunction with filters featuring narrowly tuned peaks (Linhares et al., 2008b). The chromatic diversity of 50 hyperspectral images of natural scenes was calculated in conjunction with 9 filters, 8 of them commercially available sunglasses with broadband attenuation, and one hypothetical filter with two narrowly tuned transmittance peaks around 530 and 650 nm. For normal trichromats the ratio of discernible colours without the narrowly tuned filter
to those discernible with this filter was 1.5, a substantial increase in chromatic diversity.
Although this model identified enhancement in the context of normal trichromacy, not
anomalous trichromacy, it gives credence to the potential for filters that restrict the light
in particular regions of the spectrum for the benefit of chromatic signals.

Kovacs et al., predicted the changes to individual cone activations of a hypothetical
deuteranomalous observer when CRT phosphors are attenuated by filters (Kovacs et al.,
2001). The aim was to identify a filter profile that would create relative deuteranomalous
cone activations that resemble those of a normal trichromatic observer viewing the
unfiltered RGB emissions. The optimal six-segment filter profile was identified through
a damped least-squares method (Meiron, 1965; Robb, 1979). The optimal hypothetical
filter featured ~50 to 70% transmission across the spectrum with a notch allowing 0%
transmission from 570 to 610 nm, largely cutting out the portion of the spectrum where
the spectra of the monitor’s red and green primaries overlap. Kovacs et al. simulated a
deuteranomalous observer by replacing the M cone sensitivity function with the
sensitivity function of an L cone shifted 10nm (Kovacs et al., 2001). The filter profile
derived was capable of producing anomalous LMS cone activations from CRT monitor
spectra which were far closer to those of a normal trichromat. The authors suggested
that this approach would only function for RGB displays, but with adjustment the
method would be appropriate for any variant of RGB display, including LCD and TFT
screens.

The first practical deployment of notch filters for the amelioration of CVD were
developed by EnChroma, who built notches into the neutral density filter of sunglasses.
The majority of EnChroma filters feature two notches, a primary notch in the spectral region where the anomalous cone is sensitive and a secondary notch to address the white balance, which coincides with the sensitivity function of the S cone. The design described in the 2014 patent (Schmeder & McPherson, 2014) includes a 40 nm wide primary notch centred at 580 nm, and a secondary 40 nm wide notch centred at 490 nm. Since 2012, EnChroma have produced products with a range of attenuation levels, intended for use in direct sunlight (Cx3 type), overcast (Cx2 type) and artificial indoor lighting (Cx1 type). This main range of products are intended for use by any form of anomalous trichromat, with additional high-attenuation filters targeted at strong-protonomalous (Cx2-P, Cx3-P) and strong-deuteranomalous observers (Cx3-D, enchroma.com, 2018).

Tests of the effectiveness of EnChroma filters for improving performance on tests for CVD have generally found mixed results. The EnChroma filters have been found to confer no significant improvement in tests for CVD done on screens, such as the ColorDx, a digital version of the Ishihara plates test and the digital FM100 test (Almutairi et al., 2017; Kitchens & Cisarik, 2016), but significant improvements were found in physical versions of similar tests (Varikuti et al., 2020). For the physical FM100 there appeared to be trade-offs between different regions of the spectrum, with a reduction in mean error scores in the blue-green/blue/purple-blue regions counteracted by significant increases in the yellow/green-yellow region. This suggests that there is a different impact of the filters on perception of different colours. This finding was supported by a later study of the effect of EnChroma filters on FM100 scores (Pattie et al., 2017), where FM100 test results indicated a shift in the confusion axis of deuteranomalous errors.
towards that of protanomalous observers, suggesting an alteration in the hues confused, rather than a reduction in confusion.

Gomez-Robledo et al. (2018) combined behavioural tests using CVD diagnostic tests with a modelling approach and found equally limited effects of the notch filters on anomalous trichromatic colour vision. The model used to represent the anomalous colour vision employed an approach used to simulate the appearance of anomalous colour vision for normal trichromatic observers (Lucassen & Alferdinck, 2006) by combining normal trichromatic cone activities in proportions designed to reflect certain severities of anomalous trichromacy. This method is not an effective way to examine the ability of wavelength-specific filters to alter the quantal catches of anomalous cones, as the quantal catches are calculated for the normal trichromatic cone classes which are then combined in various proportions to ‘simulate’ anomalous trichromacy. Using the Lucassen and Alferdinck (2006) approach, the simulated anomalous cone activities were calculated in response to hyperspectral images. Findings, interpreted in terms of lightness, hue and chroma predict limited impact of the filters. The overall chroma of natural scenes showed a significant decrease despite increases in the chromas of blue hues. Investigation of the filter’s impact on hue showed a significant change in the mean angular rotation of chromaticities for all modelled trichromatic observers (anomalous and normal).
1.9 Directions for current and future research

The introduction provided an overview of current understanding of colour vision deficiencies in humans. The following section will identify some areas where more research is needed. Research assessing the EnChroma notch filters currently presents a mixed picture, with some finding limited or no improvements with the filters on performance on tests for CVD (Almutairi et al., 2017; Gómez-Robledo et al., 2018), but some identifying evidence of improvement in chromatic sensitivity (Varikuti et al., 2020, Werner et al., 2020). It is possible that if the effect of the filter is a general enhancement to colour vision signals, they will not break the specific metamerisms CVD tests deploy. Broader tests of colour vision may be needed to identify the effects of the notch filters on anomalous colour vision. This could be provided by a modelling approach, calculating the impacts of the filters for a hypothetical anomalous observer for a great variety of stimuli, providing a fuller prediction of the effects. The modelling investigation by Gómez-Robledo et al. (2018) predicted no substantial effect of the filters on the colour vision of CVD observers. The method by Lucassen and Alferdinck (2006) used by Gómez-Robledo et al., however, did not represent the wavelength specific attenuation of the notch filters, which is the source of the filters’ functionality. Any model of the effects of EnChroma’s notch filters would need to be wavelength specific and physiologically accurate. Such a model could be used to design behavioural tests of the filter’s effect on anomalous colour vision, and to predict the variation in the filters’ effectiveness for observers with differing severities of anomalous trichromacy.

The literature assessing the chromatic variation of the Ishihara plates caused by illumination and other factors has some limitations. Since the plates have been in
widespread use for over a century, much of the research assessing the impact of illumination considers illuminants that are no longer widely used (Hardy et al., 1946; Schmidt, 1952), and do not consider illuminants common in contemporary labs or clinics. The impact of illuminants has frequently been summarised by colour temperature (Schmidt, 1952), but there is potential for illuminants with uneven SPDs to have more complex effects on colour perception the Ishihara Plates for individual observers. Existing studies tend to focus on a single variable, e.g., illumination alone, or edition alone (Lee & Honson, 2003). There is a need for a modelling approach to give a comprehensive assessment of chromatic variation within Ishihara plates tests with a broader survey of editions, under different illuminants, for a range of severities of CVD, to allow comparison of the impacts of each factor. A physiologically accurate modelling approach, validated by a behavioural test, could provide valuable information on the impacts of edition and illuminant when screening for mild CVD.

1.10 Thesis Overview and research questions
This thesis considers the enhancement of anomalous colour vision signals, and how individual differences in anomalous trichromacy interacts with filters and diagnostic tests for CVD.

Chapter 2 aims to predict the impact of EnChroma’s notch filter on the chromatic signals available to anomalous trichromats using a physiologically accurate model of colour vision. The model quantifies the impact of the filter on real-world viewing conditions, comparing the effects on artificial surfaces and natural surfaces, viewed directly and on RGB displays, and the impacts of different illuminations. This paper also compares the
impacts of different EnChroma filters for observers with differing severities of anomalous trichromacy, quantifying the predicted changes in colour vision signals available to the visual system. The research questions are:

1. Do the EnChroma filters increase the chromatic signals available to anomalous trichromats?

2. How variable is the effect of the EnChroma filter for observers with different severities of anomalous trichromacy, using different EnChroma products, in differing observation conditions?

Chapter 3 presents behavioural evidence collected to test the predictions made in chapter 2, to identify whether changes in saturation as represented in the retinogeniculate colour channels predicted by the model result in changes in perceived saturation. The model was used to inform the development of a battery of behavioural tests designed to measure the impact of the filters on the colour vision of deuteranomalous observers. The research questions were:

1. Is the deuteranomalous visual system able to make use of the enhanced chromatic signals predicted by the model?

2. Do EnChroma's notch filters confer a) an enhancement in perceived suprathreshold colour saturation (particularly for the red-green axis) and b) a reduction in chromatic detection thresholds?

Chapter 4 uses the model presented in Chapter 2 to assess the effectiveness of the Ishihara Plates test for CVD under different conditions. This diagnostic test uses colours designed to be distinct for those with normal trichromatic colour vision, but
indiscriminable for those with CVD. The reliability and vulnerability of the Ishihara plates test to environmental conditions were investigated for screening those with anomalous trichromacy. We examined the reliability of the chromaticities used in 7 editions of the diagnostic test, for a variety of severities of CVD under a range of illuminants. The research questions were:

1. Are there significant differences in chromatic information available in the Ishihara plates, when comparing plates, editions and illumination conditions?

2. Do the differences in chromatic information across editions of the Ishihara plates test result in different numbers of false negative diagnoses?
1.10.1 Paper 1: Modelling the effectiveness of EnChroma notch filters for improving colour vision in anomalous trichromacy

A colour vision aid has the potential to confer a life-changing and deeply emotive transformation in visual experience. Previous research which found notch filters have no significant effect on anomalous colour vision used methods of modelling vision that are not appropriate for identifying the effectiveness of notch filters. The existing modelling approach was not physiologically accurate and could not capture the wavelength-specific interactions between notch filters and anomalous cone sensitivity functions. To address this limitation in the literature, we constructed a physiologically accurate model of colour vision to predict the cone-opponent signals available to anomalous trichromats without and with the EnChroma filter.

For a holistic assessment of the effectiveness of the EnChroma filters, the model was used to predict changes in cone opponent signals for protanomalous and deuteranomalous observers in response to two datasets, a set of Munsell surfaces, and a set of 75 hyperspectral images of natural scenes. The impact the EnChroma filters on viewing images rendered on RGB displays was compared to their predicted impact when viewing the same chromaticities as physical surfaces, and the impact of 5 illuminants was investigated. The effectiveness of the filters in naturalistic viewing conditions was predicted using hyperspectral images of natural scenes. The effect of variation in filter profile on the impact of EnChroma was examined by predicting the effects of different filters on the colour signals available for three example hyperspectrally imaged scenes. The effect of variation in severity of anomalous trichromacy on the impact of EnChroma
was investigated by extending the model to 13 observers, including 2 dichromats, 10 anomalous trichromats and a normal trichromat.

The model predicted that the EnChroma filters confer substantial enhancements in cone-opponent signals for deuteranomalous and protanomalous observers for the majority of stimuli tested. The strongest enhancements were predicted for Munsell surfaces under broadband illuminants (DA: 4.8-6.11% and PA: 6.82-8.6%), due to the comparatively high proportion of saturated surfaces in this dataset and the significant relationship between predicted enhancement conferred by EnChroma and unfiltered saturation (DA $r_t=0.276$, $p<.0001$; PA $r_t=0.648$, $p<.0001$). EnChroma was predicted to cause an enhancement in colour signals for anomalous trichromats for the majority of stimuli in both datasets (e.g., enhancement of 85.33% of the Munsell dataset, 89.63% of the Natural scene dataset for a deuteranomalous observer), but small changes in colour signals were predicted to be more common than large changes. The mean predicted changes in colour signals for the Natural scene dataset were lower than for the Munsell dataset due to the greater proportion of desaturated chromaticities. The predicted enhancements of colour signals by EnChroma were substantially reduced for representations on screens compared to physical surfaces. Smaller moderations of predicted signal enhancement were found for illumination, filter type and observer type.
1.10.2 Paper 2: Behavioural tests of the effectiveness of EnChroma notch filters for improving colour vision in anomalous trichromacy

Existing behavioural research investigating the effectiveness of EnChroma filters has placed disproportionate attention on the impact of the filters on the outcome of diagnostic tests for CVD. Also, existing experiments have been conducted on samples including small number of anomalous trichromatic observers, and often larger numbers of dichromatic observers, for whom the filters are not expected to be effective (Anomalous Trichromat to Dichromat ratio: 8:19 in Mastey et al., (2016) 7:19 in Patterson, (2017); 2:8 in Almutairi et al., (2017); and 18:30 in Gómez-Robledo et al., (2018)).

Modelling has revealed that EnChroma filters have the potential to provide enhancements to cone-opponent signals (Chapter 2), though it is unknown whether the predicted increase in saturation as represented in retinogeniculate colour channels will result in an increase in perceived saturation. A battery of behavioural tests were created, guided by the predictions of the model, to assess whether the predicted changes in colour signals result in changes in perceived saturation.

Three experiments were designed to identify the filter’s impact on two aspects of deuteranomalous colour perception: colour appearance and sensitivity at threshold. Experiment 1 presented 25 Munsell surfaces in an asymmetric matching task, where observers had to identify the matching colour from an array. In one condition the target was presented through the EnChroma filter and the matching array under the neutral density filter, and in the other condition, vice versa. Experiment 2 was a 4AFC target
detection task designed to identify change in colour discrimination thresholds. Targets were one of seven hues to be discriminated from white, and target saturation was manipulated in a staircase procedure. Experiment 3 used dissimilarity ratings for a set of 13 Munsell surfaces to reconstruct internal representations of colour using multidimensional scaling. Experiment 1 was run once per session as it used both filters simultaneously, whereas experiment 2 and 3 were repeated twice within each testing session, once with each filter. Two testing sessions were conducted at different timepoints, to identify the impact of habituation. The first session was conducted without prior experience with EnChroma while the second session was conducted after the participant had used the filters for a minimum of 10 hours over 4 to 8 days.

Experiment 1 identified systematic changes caused by the EnChroma filter in both the hue and chroma of Munsell surfaces identified as matches. This pattern was observed in both filter conditions, with matches of higher saturation selected when the target was viewed with the EnChroma filter and matches of lower saturation selected when the matching array was viewed with the EnChroma filter. Experiment 2 identified significant changes in colour discrimination thresholds with EnChroma, but only for red hues, suggesting that only the largest predicted enhancements were useable by the visual system, or that our test was not sensitive enough to identify impacts of the smaller predictions of the filter’s effect. Experiment 3 identified a small expansion in perceived saturation along one dimension of the participants’ MDS solutions, which did not persist after the 10 hours of habituation to the filters.
This battery of behavioural experiments present small to moderate positive effects of the EnChroma filters on anomalous colour perception. Our findings suggest that the EnChroma filter does enhance perceived saturation of suprathreshold targets for deuteranomalous observers, but that enhancements conferred at and near threshold are only partially significant.

1.10.3 Paper 3: Recommendations for the screening of mild anomalous trichromats with the Ishihara plates test

The Ishihara plates test is the most widely used screening tool for CVD. It is accessible, simple to use, and has a high sensitivity and specificity. However, the test is less effective at identifying mild cases of anomalous trichromacy. Due to a lack of screening for CVD in UK schools, the majority of mild anomalous trichromats are undiagnosed, requiring researchers intending to test this population to first carry out screening. Screening of the population at Sussex University using the Ishihara plates test resulted in an over-representation of dichromats and extreme anomalous trichromats once classified using an anomaloscope. This prompted an investigation into the factors that might be causing mild anomalous trichromats to be missed by the Ishihara plates test.

The following investigation sought to identify whether the age of test, edition, or illuminant may be influencing the sensitivity of the plates test for identifying mild anomalous trichromats. The model of colour vision presented in Chapter 2 was used to estimate the chromatic signals available to segregate figure from ground, for observers with 3 severities of anomalous trichromacy, in response to the chromaticities in 6 plates
of 7 editions of the Ishihara plates test spanning 8 decades, when viewed under 8 illuminants.

The robustness of a plate is predicted from the difference between the chromaticities of the background and those of the numeral designed to be visible to the normal trichromat but pseudoisochromatic for the CVD observer. The effect of each variation (observer, age, edition and illumination) was compared, and the predictions were tested against the results of a behavioural investigation in which 35 individuals with CVD took all 7 editions of the plates test. The model predicted that edition would have a smaller influence on anomalous trichromatic observations, but that variation between plates and illumination would both hold a significant influence that differs between the phenotypes of X-linked anomalous trichromacy. The behavioural investigation revealed a significant negative correlation between error rate and the modelled chromatic signal, indicating that the more chromatic signals available in portions of the test designed to be isochromatic, the fewer errors were made. This supports the interpretation of chromatic signal influencing the robustness of the Plates test and gives weight to the predictions of the model on the influence of illuminant and plate variation for different observers.
1.11 Overall Contribution

This thesis aims to better understand perception of pseudoisochromatic plates by anomalous trichromats and to investigate the effects of notch filters for potentially enhancing anomalous trichromatic colour vision. The findings presented here have the potential to contribute to not only research, but also to industry and to the lives of anomalous trichromats. Recommendations for the use of pseudoisochromatic plates in screening for CVD contribute to the effective identification, representation in research and support of mild anomalous trichromats. A greater understanding of filter aids for colour vision contributes to scientific understanding of the visual systems of this special population, it contributes to industry’s understanding of what possibilities there are for producing effective aids and contributes to the understanding and confidence of people with anomalous trichromacy who stand to gain from this intervention.

1.11.1 Theoretical contributions

A core contribution of this thesis is the demonstration of the effectiveness of notch-filters in enhancing both protanomalous and deuteranomalous colour vision. Substantial numbers of colour vision aids have been introduced to the market with no published evidence for their effectiveness, but the findings reported in this thesis mark an important distinction between the likely effectiveness of notch-filter aids over broadband-filter aids. Results described in Chapter 2 show that filters which preferentially alter the light within the receptive range of one cone class over another have the potential to alter cone-opponent signals, and thus impact the perceived saturation of colours.
In addition to this, findings reported in Chapter 3 contribute to existing knowledge of the adaptability and plasticity of the colour vision system. A core question beyond the concept of selectively filtering cone classes, is whether the visual system can make use of the resulting altered cone-opponent signals. By demonstrating that filtered input to the visual system results in enhanced percepts of saturation, these findings indicate that unequally filtering the cone classes does produce a useable difference in cone-opponent signals. The results also indicate that the deuteranomalous colour vision system is adaptable enough to process enhanced cone-opponent signals along neural pathways which have carried reduced chromatic signals throughout the lifespan.

A corollary to this contribution is a demonstration that increased cone-opponent signals enhance suprathreshold colour perception but have a much smaller effect on perception at threshold. Future research is needed to examine potential effects of filter-based aids on colour vision near threshold. Future research could also address the possibility for adapting the notch-filter aids for use with dichromatic observers. If subsets of retinal cones could reliably receive filtered light, it might be possible to simulate a trichromatic signal within a dichromatic observer.

1.11.2 Methodological contributions

This thesis contributes a detailed comparison of the environmental and practical factors affecting colour vision screening and the scale and significance of their impact. Flawed screening, leading to either false positive or false negative diagnoses of CVD can have lasting damaging consequences. False negatives can result in individuals failing to receive
the support they might need and would contribute to mild anomalous trichromats being a difficult-to-access population for research purposes, resulting in the population being underrepresented in scientific investigation and understanding. False positives can have equally problematic impacts for research and can have substantial personal impacts for the individual.

A key component of this thesis’ contribution is in identifying how factors affecting performance on the Ishihara Plates test may differ between types and severities of anomalous trichromacy, since the literature typically does not differentiate between phenotypes in existing screening recommendations. Knowing more about how different CVD groups perform on screening tests will inform best practise and increase the effectiveness of screening, particularly for mild anomalous trichromacy.

1.11.3 Applied contributions

This thesis contributes knowledge and understanding that will be of value to industry and society, by validating the notch filter as an effective means of aiding the colour perception of anomalous trichromats. Empirical support for the effectiveness of notch filter aids will be of interest to the wider public, and especially the ~180 to ~340 million anomalous trichromats who stand to benefit from these aids (extrapolated from Birch, 2012). A better understanding of the filters’ effectiveness and limitations will allow anomalous trichromats to better assess them as a substantial personal investment. Detailed investigation into this technology’s function and its limitations will inform future development, testing and refinement of future aids. As new visual display
technologies are developed, there is a great need for these to be developed with accessibility in mind and understanding the implications of RGB digital displays as well as spectral filters can potentially improve the development of products and the visual experience of anomalous trichromats.

Future research could determine the wellbeing impact of longer term use of notch filter aids in addressing the negative association between indices of quality-of-life and colour vision deficiency, and by investigating the effectiveness of the intervention in other applications, such as notch filtered lighting. Lighting applications carry great potential for passively increasing safety, accessibility, and inclusion for anomalous trichromats in a wide range of settings.
Chapter 2: Modelling the effectiveness of EnChroma notched filters for improving colour vision in anomalous trichromacy

2.0 Abstract

Notch filters built into sunglasses are being marketed as aids to alleviate colour vision deficiency (CVD). These aids are a commercial success, with enthusiastic customer testimonials in contradiction to the limited evidence available indicating that the glasses have no significant effect on performance in diagnostic tests for CVD. To clarify this contradiction, we modelled the effect of the glasses on a broader range of stimuli than previously tested, using a physiologically accurate model of anomalous trichromatic vision. Using the model, we established predictions of the strength of signals carried by the cone-opponent colour mechanisms for different combinations of EnChroma filters, illuminations, reflectances and observers. A dataset of 259 Munsell reflectance spectra were used in the model to assess how the EnChroma filter affects chromatic signals for broadband surfaces under different illumination conditions, and for the same surfaces presented on RGB monitors. A second dataset of 75 hyperspectral images were used to predict the impact of the filters on perception of natural scenes. The model predicted substantial increases in cone-opponent signals for deuteranomalous and protanomalous observers in the majority of scenarios tested, presented as change in signal as a proportion of 99.8% of the natural scene gamut. The strongest enhancements were identified in response to Munsell surfaces under broadband illuminants (mean signal change for deuteranomals (DA): 4.80-6.11% and protanomals (PA): 6.82-8.60%), due to the comparatively high proportion of saturated surfaces in this dataset and the significant
relationship between colour signal enhancement and unfiltered saturation (DA \( r = .276 \) \( p<.0001 \), PA \( r = .648 \) \( p<.0001 \)). The majority of samples from both datasets were predicted to receive an enhancement in signal (85.3% of the Munsell dataset, 89.6% of the Natural scene dataset), with small signal enhancements more common than larger signal enhancements. The mean predicted signal changes for the Natural scene dataset was lower than for the Munsell dataset, and enhancements were predicted to be substantially reduced for representations on screens. There were smaller moderations of predicted signal enhancements for illumination, filter variation and observer. The findings of this model are predictions of saturation as signalled by the cone opponent mechanisms. The implications for perceived saturation are tested in a partner paper presenting behavioural corroboration of the model’s predictions (see Chapter 3).

2.1 Introduction

Notch filters selectively attenuate certain bands of wavelengths of light while allowing transmission at wavelengths either side of the attenuated bands of wavelengths. The deleterious effects of anomalous trichromacy compared to normal trichromacy occur because the sensitivity functions of two cone types sensitive in the medium and longwave part of the spectrum overlap to a greater degree than in normal trichromacy. The use of notch filters as a way to enhance anomalous colour vision is based on the premise that the difference in signals of these cone types can be increased by filtering out light in the spectral region where their sensitivity functions are most similar.
Andrew Schmeder and Don McPherson (EnChroma, Berkeley, USA; Schmeder & McPherson, 2014) were granted a patent for the use of multi-notch filters as wearable colour vision aids for anomalous trichromats, in which one of the notches is engineered to coincide with the region of the spectrum in which the sensitivity functions of the of the medium and wavelength sensitive cone fundamentals (one anomalous) overlap. This is intended to increase the difference between the activities of the two medium and long wavelength sensitive cone types, and correspondingly increase signals in the L/(L+M) cone opponent colour mechanism. Here, using a physiologically accurate model of anomalous colour vision we estimate the effectiveness of EnChroma’s multi-notch filters for a variety of combinations of filter, observer, and incident spectra to quantify their expected effectiveness for a range of stimuli, including natural scenes.

2.1.1 Anomalous Colour Vision

Normal human colour vision is based on the responses of three types of retinal cone, maximally sensitive to short- (S), medium- (M) and long- (L) wavelengths of light. Post-receptormally, two ‘opponent’ colour mechanisms receive opposing inputs from the different cone types. The ancestral S/(L+M) subsystem compares the activities of the S cones with the combined activities of the M and L cones (Jameson & D’Andrade, 2009; Mollon, Estévez, et al., 1990). The more recently evolved L/(L+M) subsystem compares the activities of the L cones with that of the M cones (Mollon, Estévez, et al., 1990).

Congenital ‘red-green’ colour vision deficiency (CVD) occurs when the L or M cones are absent or abnormal, resulting in disruption to the L/(L+M) opponent pathway. In dichromacy either the L or M cone type is absent or non-functional and colour vision is
one dimensional, relying on the S-cone subsystem only. An absence of the L cones results in *protanopia* (affecting 1% of men and 0.01% of women; Sharpe et al., 1999), while an absence of the M cones results in *deuteranopia* (affecting 1% of men and 0.01% of women; Sharpe et al., 1999). In the milder *anomalous trichromacy*, three different cone types are present, and so two-dimensional colour vision based on two cone-opponent subsystems is retained, but one cone type has a spectral sensitivity different from the norm. In deuteranomaly, affecting about 5% of men and 0.35% of women (Sharpe et al., 1999), the L opsin is present as normal but the M opsin is replaced by an opsin we will call L’, with a peak spectral sensitivity close to that of the normal L cone. Similarly, in protanomaly, affecting 1% of men and 0.03% of women (Sharpe et al., 1999), the normal M opsin is present but the L opsin is replaced by an anomalous opsin, which we will call M’, with a peak sensitivity close to that of the normal M cone.

Owing to the greater spectral overlap between the sensitivity functions of long and medium-wavelength sensitive cone types, there is a smaller difference between the responses of the two cone types in anomalous trichromats, than between the L and M cones of normal trichromats. This results in reduced colour discrimination, negatively impacting anomalous trichromats’ ability to make colour-based judgements which occur through all facets of life. Individuals with colour vision deficiency face limitations to their career opportunities, as numerous professions require the discrimination of coloured safety features, and difficulties performing day to day tasks, such as judging the ripeness of fruit and rawnness of meat, selecting decorations, or making decisions that require discrimination at speed, such as when driving (Steward & Cole, 1989). The detrimental
effect the perceptual limitations have on performance can lead to anxiety, low self-esteem, with broad impacts on quality of life (Stoianov et al., 2019).

2.1.2 Filter-based aids for CVD
Filters have been used to try to enhance the colour vision of anomalous trichromats for several centuries. Early incarnations employed interocular discrepancy; attenuating the light to each eye differently to introduce interocular luminance cues. Seebeck (1837) pioneered this method by placing a green filter in front of one eye and a red filter in front of the other, noting that the unequal attenuation by the two filters introduced a binocular lustre (Wendt & Faul, 2022) which allowed the discrimination of previously indistinguishable colours. This concept was adopted and developed into commercial products for Chromagen (Birkenhead, United Kingdom; (D. A. Harris, 1999), Colormax, (Birmingham, Alabama USA, no patent published) and X-Chrom, (Ipswich, Massachusetts USA; (Zeltzer, 1991). ChromaGen, Colormax and X-Chrom offer contact lenses that claim to provide filters tailored to the specific type of anomalous trichromacy that affects the wearer. These interventions do not enhance the colour vision of the wearer (Ilhan et al., 2020; Sheedy & Stocker, 1984), but allow enhanced performance in pseudo-isochromatic tests of CVD by introducing luminance cues which break the metamerisms intended to identify colour vision deficiency (Ilhan et al., 2020; Sato et al., 2019). These interventions allow the discrimination of some previously indistinguishable hues on the basis of a luminance signal but do not enhance the wearer’s colour sensitivity (Sheedy & Stocker, 1984).
A later strategy involves using filters to attenuate light from specific portions of the visible spectrum. These filters vary greatly in spectral profile to block light selectively in particular portions of the spectrum. This is achieved by combining multiple filters in the case of the Colorlite aid (Ábrahám et al., 1998), with other approaches utilizing the narrow spectral absorbance of a single material or dye (Elsherif et al., 2021; Schmeder & McPherson, 2015). The Colorlite filters developed by Ábrahám and Wenzel (Colorlite, Budapest, Hungary; Ábrahám et al., 1998) consists of a range of 10 filters to be used in differing combinations to optimally enhance differing cases of anomalous trichromacy. Despite being the earliest development of notch filters as a colour vision intervention (Ábrahám, 2001), there is limited research testing their effectiveness. The research there is has been carried out on single filters in isolation, rather than combination (Moreland et al., 2010). Moreland modelled the impact of 10 Colorlite filters on chromaticities for the DeMarco et al. standard observers (DeMarco et al., 1992), finding limited results that may in part be due to the fact that the observer used in the model was inappropriate for the majority of the filters. 10 Colorlite filters were also assessed by Martinez-Domingo et al., (Martínez-Domingo et al., 2020), who concluded that the filters decrease chromatic diversity for deutan and protan anomalous trichromats and dichromats.

Notch filters selectively attenuate light from narrow spectral wavebands, allowing transmission at wavelengths either side of the notch. The intent of this approach is to differentially attenuate the light reaching the two cone classes whose sensitivities which are more closely overlapping in anomalous trichromacy than in normal trichromacy. This selective attenuation affords a greater functional difference between their sensitivity functions. EnChroma constructs notch filters using neodymium, a rare earth metal which
features narrow notches of spectral attenuation at 520 and 590 nm. Originally developed in partnership with Barber and Changizi who went on to develop Oxy-Iso notch filters for medical devices aimed at enhancing the appearance of blood (Oxy-Iso, Boise, Idaho USA; Barber & Changizi, 2012). The Oxy-iso filters employ the same principle as used in EnChroma products, altering the ratio of signals from anomalous x-linked cone types, to simulate a greater difference in the cone absorbances by attenuating spectral transmittance. Barber and Changizi’s filters feature a wider notch to enhance the discrimination of red hues for the normal trichromatic observer, to aid the discrimination of blood oxygenation levels in clinical and medical settings (Barber & Changizi, 2012).

Since becoming commercially available in 2012, the products offered by EnChroma have been modified repeatedly. Early product lines featured ‘colour enhancing’ filters for normal trichromats as well as colour deficient observers (enchroma.com 2012-2014, accessed via archive.org), but later filters were designed for colour deficient observers only. Initially filters at three broad levels of light attenuation (enchroma.com, 2016), but at the time of writing two filter types are offered, aimed at indoor (Cx-65) and outdoor (Cx-25) use (enchroma.com, 2018-2022). The spectral profiles of the notches themselves have also varied over time and over the range of products: Figure 1 shows the transmittances of 16 examples of Cx-25 EnChroma products between 2017 and 2018. All filters feature a main functional notch around 570nm, and a white-balancing notch around 490nm, with variation mostly found in the width and attenuation levels of these notches.
Figure 1. Transmission spectra of 16 EnChroma filters. Transmission profiles are grouped into three main categories classified as “high transmission” filter, for their overall higher transmission, “low transmission” filter class characterised by higher levels of attenuation, and “triple notch” filter, which feature an additional notch at ~645 nm, not present in other filter profiles.

Two novel methods of constructing filters with narrow high-attenuation notches from ATTO dyes (Badawy et al., 2018; Elsherif et al., 2021) and gold meta-surfaces (Karepov & Ellenbogen, 2020) are currently in development. These approaches have the potential to deliver cost effective notch filter contact lenses but are yet to be deployed and tested.

2.1.3 Existing models of the effectiveness of filter-based aids for CVD
Modelling is an established approach to enable estimations of the impacts of external interventions on the internal signals of the visual system. Although models cannot be
perfect tools for the prediction of effects, they enable us to examine the impacts of an intervention accounting for many variables such as observer, reflectance, light and filter type. Cone sensitivity functions have been estimated by a succession of researchers (DeMarco et al., 1992; Smith & Pokorny, 1975; Stockman & Sharpe, 2000), as well as the wavelengths of peak sensitivity of opsin variants (Merbs & Nathans, 1992a, 1992b). It is possible to represent colours in a colour space based on the visual signals available in the cone-opponent mechanisms, such as the MacLeod Boynton (1979) chromaticity diagram, which can be easily adapted for individual observers by substituting observer-specific cone fundamentals.

Anomalous trichromatic versions of the MacLeod Boynton (1979) chromaticity diagram have been used in a previous attempt to model the effects of colour vision aids for anomalous trichromats by Moreland et al. (2010), who examined Colorlite (Budapest, Hungary), X-Chrom (Ipswich, Massachusetts USA), Chromagen (Birkenhead, UK), and Colourmax (Birmingham, Alabama USA) filters. They modelled anomalous colour vision by calculating cone activities from cone sensitivity functions for protanomalous and deuteranomalous standard observers (DeMarco et al., 1992) in response to the radiances of controlled illuminants and known surface reflectances from the Farnsworth-Munsell D-15 test for CVD (Farnsworth, 1943a). From these cone responses they estimated the signals carried by the anomalous equivalents of the $S/(L+M)$ and $L/(L+M)$ cone-opponent subsystems. They presented the impact of the filters as in terms of predicted enhancement or attenuation of signals in these subsystems separately, with the criterion for a useful signal increase as two times the ratio of “aided” to “unaided” standard deviations. This criterion was not reached with any of the filters tested, and all were
found to attenuate traffic signals to below the luminance required by European Safety Standards (CEN, 2007).

Gómez-Robledo et al. (2018) tested the effectiveness of an EnChroma filter using a method better suited to the simulation of CVD for normal trichromatic observers than a model of colour vision in anomalous trichromacy of different levels of severity. Their work is based on a model by Lucassen and Alferdinck (2006) which combines proportions of normal trichromatic L and M cone activities to estimate the activities of cone types with intermediate spectral sensitivities. Mild deuteranomaly, for example, was simulated by merging 30% of the activity of a normal trichromatic L cone with 70% of the activity of the normal trichromatic M cone. This method goes some way towards representing the reduction in cone-opponent signals in anomalous trichromacy but does not accurately reflect wavelength-specific changes in sensitivity and does not accurately model the interaction between the anomalous cone fundamentals and the wavelength-specific notch of the EnChroma filter. Gómez-Robledo et al. (2018) assessed the impact of the filters on simulated observer representations of median lightness, median chroma and mean hue angle for their stimulus datasets. Their model predicted that the EnChroma filters slightly decrease median lightness for all deutan observers and slightly increase it for protan observers (luminance adaptation was accounted for in the model). The chroma of uniform stimuli significantly increased for all observer types, however the model predicted the opposite trend for hyperspectral images, with the chroma of natural scenes decreasing significantly for all observers. The effect of EnChroma filters on hue was assessed in terms of mean angular rotation in CIECAM02: there was a mean counterclockwise shift for mildly anomalous observers and a mean clockwise shift for strongly
anomalous observers. They found that the EnChroma filter contributed small but significant changes to the lightness, hue and chroma of their simulated stimuli, but concluded the changes were so small that only a subset would be perceptible, calling into question the overall effectiveness of the filters.

Our model implements a more physiologically accurate model of colour vision which preserves the wavelength-specific interaction of the notch filter and the anomalous trichromatic cone sensitivity functions. We use our model to estimate the effectiveness of EnChroma filters using a broad dataset of ecologically valid stimuli. In an accompanying paper we also present the results of psychophysical experiments to test the validity of the model and test the effect of the filters on the perception of real human observers (Chapter 3).

2.2 General Methods

2.2.1 The model
We created a model of colour vision for any combination of illumination, surface, filter, and observer. Figure 2 depicts the stages of the model. The radiance spectrum from a given illuminant (1) is attenuated by the reflectance spectrum of a given surface (2), before passing through an EnChroma filter (3) which further attenuates the energy that then reaches the eye of an anomalous observer. The observer has a set of cone spectral sensitivity functions shown normalised in (4) to peak at 1 but are scaled in the model as for the Smith and Pokorny (1975) standard observer (scalings are different for results reported in Section 2.8, see Section 2.2.2.4 for details). The cone sensitivity functions
are multiplied by the incident spectrum to estimate each cone’s response to the light at each wavelength (5). The activity of each cone class is summed over wavelengths to give the total cone response to the light (6). Retinogeniculate cone-opponent signals are then estimated as MacLeod Boynton (1979) chromaticity coordinates $S/(L+M)$ and $L/(L+M)$ (7). The model is summarized in Equation 1 a), b) and c), where $I(\lambda)$, $m(\lambda)$ and $s(\lambda)$ are the three cone sensitivity functions available to a given observer (note that for deuteranomalous observers the three cone types are denoted L, L’ and S, and for protanomalous observers they are denoted M’, M and S). $R(\lambda)$ is the reflectance spectrum, $I(\lambda)$ is the illumination spectrum, and $\tau(\lambda)$ is the transmission spectrum of the EnChroma filter. L, M and S are the tristimulus cone responses to the combination of illumination, reflectance, and filter.

![Figure 2](image)

*Figure 2. Step by step depiction of the model used to calculate the impact of notch filters on the observer-specific chromaticities of surfaces. The spectral energy reflected from the surface is calculated by attenuating the illuminant spectrum (1) by the reflectance spectrum of the surface being viewed (2). Combined, these form the radiance spectrum, which is further attenuated by the transmission spectrum of the notch filter (3) as the light passes through the EnChroma glasses. The responses per wavelength of the cones (4) are calculated using sensitivity functions for the anomalous observer (5). Cone
responses per wavelength are then summed to give the activities of the three cone classes (6). These are then plotted in a variant of the MacLeod Boynton (1979) chromaticity diagram (7) constructed for the particular anomalous trichromat observer.

Equation 1:

\[ L = \int_{380}^{780} l(\lambda) R(\lambda) I(\lambda) \tau(\lambda) \, d\lambda \]

a)

\[ M = \int_{380}^{780} m(\lambda) R(\lambda) I(\lambda) \tau(\lambda) \, d\lambda \]

b)

\[ S = \int_{380}^{780} s(\lambda) R(\lambda) I(\lambda) \tau(\lambda) \, d\lambda \]

c)

The EnChroma filter is designed to selectively attenuate certain wavelengths of light, in order to increase the difference between the activities of the two x-linked cone classes. The effectiveness of this intervention is likely to be influenced by all components represented in the model. Polymorphic versions of genes for the long and medium wavelength-sensitive opsins alter the cone sensitivity functions, meaning that observer phenotype may have an impact on the effectiveness of the EnChroma filters. The spectral power distribution (SPD) of the illuminant may also have an impact, as may the reflectance spectrum of the surface being observed, as well as whether the stimuli are viewed as physical surfaces or on RGB monitors. The variables manipulated in the model are introduced in the following section.
Figure 3. Relative cone sensitivities of the deuteranomalous observer represented by L and S cone fundamentals from Smith & Pokorny (1975) and L' cone fundamental from DeMarco et al., (1982). The transmission spectral profile of the EnChroma filter is indicated by the green area.

2.2.2 Variables in the model
Since the effect of the multi-notch filter depends on all the variables included in the model, we investigated the impact of reflectance, illumination, observer and filter separately. Section 2.3 presents the impact of the SPD of surface reflectance on how EnChroma alters colour signals in response to a range of uniform chromatic stimuli taken from the Munsell Atlas (X-rite, Massachusetts, USA). In Section 2.4, we model the effect of EnChroma on the same surfaces rendered on RGB displays. In Section 2.5, the impact of different illuminations is presented, with two natural daylight illuminants compared to four artificial illuminants with differing amounts of power in the spectral regions of the filter’s notches.
In Section 2.6 model is extended to investigate the impact of the filters on colour perception in more naturalistic conditions. We used a dataset of natural scenes comprised of 75 hyperspectral images, providing the ability to assess the impact of the EnChroma filters on a far larger dataset than the Munsell Atlas, with an ecologically valid distribution of surface reflectances and illuminants.

In section 2.7 variability within the EnChroma product line is assessed, with three filter profiles compared according to their impacts on chromatic signals in response to both the uniform surface and hyperspectral datasets.

In section 2.8 variation within deuteranomalous and protanomalous observers is investigated by comparing the effects on six variants of anomalous trichromacy, normal trichromacy and dichromacy.

In each section, one variable is manipulated while others are held constant. Where variables are held constant, ‘default’ conditions are applied.

2.2.2.1 Spectral datasets

We used three spectral datasets:

Dataset 1: Uniform broadband stimuli
Dataset 2: Stimuli rendered on RGB displays
Dataset 3: Hyperspectral stimuli.

Dataset 1 is the full set of Glossy Munsell surfaces with a Value of 5 (N=259) obtained from the online-accessible dataset of 1600 Glossy Munsell surface reflectances provided
by the University of Eastern Finland (Orava, https://sites.uef.fi/spectral) with a resolution of 1 nm for the range 380 nm to 780 nm.

Dataset 2 is populated by samples from Dataset 1 converted into simulations of the surfaces rendered on RGB displays. The broadband SPDs were converted into RGB triplets, and then the resulting RGB SPD was calculated by summing relevant proportions of the SPDs of the three display primaries. Rendered stimulus spectra were calculated for three RGB display types; a cathode-ray tube (CRT), an in-plane switching liquid crystal display (IPS LCD) and a light emitting diode backlit liquid crystal display (LED LCD). The SPDs of the display primaries were recorded for each display type using a PR655 SpectraScan spectroradiometer (Photoresearch, Chatsworth, CA). Dataset 2 was interpolated to have a resolution of 1 nm for the range 380 to 780 nm.

Dataset 3 is a selection of 75 hyperspectral images (see Table 7 in Section 2.6.1 for their sources). Each pixel is referred to as a sample (N=50,930,067). Samples were combined across all hyperspectral images, and then the lowest luminance (0.5%) samples were removed from the set. The removal of the lowest luminance pixels was done to remove artifacts such as noise from the recording devices. All hyperspectral data had a spectral resolution of 10 nm from 400 nm to 700 nm. Data not originally in 10 nm resolution was interpolated.

2.2.2.2 Illuminants

The default illuminant, LED, is used in all sections apart from Section 2.4, in which light from the simulated displays is the only illuminant present, and Section 2.5, in which illumination is varied, and Section 2.6, in which hyperspectral images retain the
illuminations recorded in the imaged scenes. The illuminants compared in Section 2.5 are LED, halogen, blue daylight, yellow daylight, and fluorescent.

2.2.2.3 Filters

The default experimental filter is referred to as the “low transmittance” filter. This filter is used in all sections other than Section 2.7, in which two additional EnChroma filters characterized as “high transmittance” and “triple notch” are compared to the low transmittance filter. The default low transmittance filter was measured using a PR655 SpectraScan spectroradiometer (Photoresearch, Chatsworth, CA) and a standard white surface (polytetrafluoroethylene, Sphere Optics, Uhldingen, Germany).

2.2.2.4 Observers

In all sections where the observer is not being investigated, the default observer is a ‘standard’ deuteranomalous observer (Figure 3) featuring S, L’ and L cones, where the S and L cone sensitivity functions are from Smith and Pokorny (1975), and L’ sensitivity function is from DeMarco et al. (1992). The modelled protanomalous observer has S, M and M’ cone sensitivities, with the S and L sensitivity functions from Smith and Pokorny (1975), and M’ sensitivity function taken from DeMarco et al. (1992).

In Section 2.8, the impact of observer variation on the effectiveness of EnChroma filters is investigated by comparing the output of the model for a range of hypothetical anomalous trichromatic observers of varying severities. These observers were simulated using a nomogram (Stockman & Sharpe, 2000) to model five severities each of deuteranomaly and protanomaly. These observers feature $\Delta \lambda_{\text{max}}$ (the spectral difference between the peak sensitivities of the two medium or long wavelength sensitive cone
types) spanning the typical range found in anomalous trichromacy (Bosten, 2019): 1 nm, 3 nm, 6 nm, 9 nm and 12 nm.

The simulated sensitivity as a function of log wavelength $\text{Log}_{10}(S(x))$ is calculated according to Equation 2, where $a = -188862.97$, $b = 90228.97$, $c = -2483.53$, $d = -6675.01$, $e = 1813.53$, $f = -215.18$, $g = 12.49$, and $h = -0.29$. Cone fundamentals with different values for $\lambda_{\text{max}}$ are created by shifting the template along the log frequency scale ($x = \log_{10}(\lambda) - \log_{10}(\lambda_{\text{max}}/558)$).

\[
\text{Log}_{10}(S(x)) = a + bx^2 + cx^4 + dx^6 + ex^8 + fx^{10} + gx^{12} + hx^{14}
\]

\(\text{Equation 2. Stockman and Sharpe (2000) nomogram for creating template cone fundamentals.}\)

Pre-receptoral filtering was modelled using the macular pigment transmittance function used by Stockman, Sharpe and Fach (1999), and a lens transmittance function calculated for a 20-year-old observer using equations provided by Pokorny et al. (1987). Optical densities were estimated as 0.38 0.38, and 0.3 for L, M and S cones, respectively (Stockman and Sharpe, 2000). Scaling factors were applied before the pre-receptoral filters to replicate the relative sensitivities of the Stockman and Sharpe (2000) fundamentals for the 20-year-old observer. In addition to the anomalous trichromatic observers, the nomogram was used to simulate a normal trichromatic observer with a $\Delta\lambda_{\text{max}}$ of 28.6 nm, and two dichromatic observers, with the same pre-receptoral filtering as the simulated anomalous trichromats.
2.2.3 Output of the model

We present results in variations of the MacLeod Boynton (1979) chromaticity diagram, amended so that the axes represent the cone opponent signals available to the deuteranomalous and protanomalous visual systems. The axes of this chromaticity diagram represent the signals of the two cone opponent subsystems separately; the ordinate represents \( S/(L+M) \), ranging from chartreuse to violet, and the abscissa represents \( L/(L+M) \) ranging from teal to cherry. In the anomalous versions of this chromaticity diagram the abscissa represents the signal available to the anomalous observer from their equivalent subsystem: \( L/(L+L') \) in deuteranomaly, and \( M'/(M'+M) \) in protanomaly. The MacLeod-Boynton (1979) chromaticity diagram is particularly useful in the context of our model for interpreting the effects of the multi-notch filters, as the impact of the filters on the impaired subsystem in anomalous trichromacy is isolated to the horizontal axis. The axis representing S cone signal is scaled arbitrarily, and thus it is important not to make direct comparisons between the sizes of signals in the \( S/(L+M) \) and \( L/(L+M) \) subsystems.

2.2.3.1 Chromaticities expressed relative to the white point

We translate the chromaticities in our variants of the MacLeod-Boynton (1979) chromaticity diagram to be centred at the achromatic point (coordinates 0,0). Thus, our model outputs chromaticities in terms of difference in signal relative to the achromatic point, e.g., as \( L/(L+M)_w \). Any chromaticity along the \( L/(L+M)_w \) axis that is greener than the achromatic point is negative, and any chromaticity redder than the achromatic point is positive. For the Munsell dataset (datasets 1 and 2), the white point was defined as
the lightest neutral chip (‘Neutral 9.5’). For the hyperspectral dataset (dataset 3), the white point was defined as the mean chromaticity for each scene.

2.2.3.2 Saturation

Changes in chromaticities away from the achromatic point in the MacLeod-Boynton (1979) chromaticity diagram describe changes in what we call ‘saturation’. However, the model simulates only retinal colour signals, and does not provide an accurate model of colour appearance. Changes in perceived saturation may be different from changes in signals carried by the modelled cone-opponent mechanisms, as contrast adaptation as well as any nonlinearities in cortical colour representation may have an impact. The model requires validation from behavioural experiments to determine whether any predicted changes in saturation as represented in the cone opponent mechanisms result in comparable changes in perceived saturation (see Chapter 3). The majority of the findings in this investigation are presented in terms of predicted changes in cone opponent signals, describing the impacts of the filter mainly in terms of our model of ‘saturation’ as it is represented in retinogeniculate colour pathways, rather than hue or luminance.

In the MacLeod Boynton (1979) chromaticity diagram, saturation increases with distance from the achromatic point, located in the centre of the space, with the greatest saturations occurring at the negative extremes as well as positive extremes of the L/(L+M) and S(L+M) axes. Our model of the effect of the EnChroma filter on these signals calculates the change in saturation along each cardinal axis and we thus use a chromaticity coordinate system specified relative to a white point. To achieve this, we translate the
MacLeod-Boynton chromaticity diagram so it is centred on a white point at (0,0). We refer to these coordinates as \( \frac{L}{L+M} \) and \( \frac{S}{L+M} \). To quantify the effect of the EnChroma filter we then collapse across the two poles of an axis (e.g. increments and decrements in \( \frac{L}{L+L'} \)) and thus present changes in *absolute* cone opponent signals conferred by EnChroma, i.e., for the deuteranom al, \( \Delta(\frac{L}{L+L'}) = |\frac{L}{L+L'}|_E - |\frac{L}{L+L'}|_w \), where \( \Delta(\frac{L}{L+L'}) \) is the change in \( \frac{L}{L+L'} \) saturation conferred by EnChroma, \( |\frac{L}{L+L'}|_E \) is the \( \frac{L}{L+M} \) saturation of the target with EnChroma and \( |\frac{L}{L+L'}|_w \) is the \( \frac{L}{L+M} \) saturation of the target without EnChroma. Using this metric any increase in saturation as a result of the filter is positive, while any decrease is negative. Thus, any systematic increase in absolute \( \Delta(\frac{L}{L+L'}) \) signals represents ‘gamut expansion’ and suggests an increase in chromatic diversity, while any systematic decrease in absolute \( \Delta(\frac{L}{L+L'}) \), represents ‘gamut contraction’, and suggests a decrease in chromatic diversity.

2.2.3.3 Defining the scale of changes in signals

We define the scale of the effect of the filters using a comparative measure (Equation 3), which situates the effect in relation to an estimated chromatic ‘visual diet’ consisting of the 99.8\(^{th}\) percentile of absolute \( \frac{L}{L'+L} \) signals (\( \frac{L}{L+M} \) saturations) present in the 75 hyperspectral images of natural scenes (without EnChroma) which make up Dataset 3. We chose for the denominator to be the 99.8\(^{th}\) percentile of aggregated absolute \( \frac{L}{L'+L} \) signals across all 75 scenes rather than the 99.8\(^{th}\) percentile of absolute \( \frac{L}{L'+L} \) signals for each individual scene to prevent the effect sizes for
individual scenes being influenced by the different chromatic gamuts. Having the same denominator for all scenes also allows direct comparisons between scenes.

Equation 3:

\[
\Delta \frac{L}{(L'+L)} \% = \left( \frac{\Delta \frac{L}{(L'+L)}}{\frac{L}{(L'+L)}_{99.8\%}} \right) \times 100
\]

We chose the 99.8\textsuperscript{th} percentile of absolute \(L/(L'+L)_w\) signals in the scenes for the denominator in Equation 2 rather than the 100\textsuperscript{th} percentile (full saturation gamut) because the most extreme 0.1\% of pixels contained a high proportion of outliers, which may be attributable to chromatic noise in the images and were not considered part of a common ‘visual diet’. Thus, the effect sizes we report here are scaled by the denominator in Equation 3. For example, any reduction in the denominator (e.g. to 75\% of the typical ‘gamut’ of \(L/(L'+L)_w\) in the hyperspectrally imaged scenes) would increase the effect sizes we report for the influence of the multi-notch filters.

![Figure 4. Examples of locations within hyperspectral images of the most extreme 0.2% of L/(L'+L)_w saturations in our dataset. The chromatic gamut used as the denominator was defined as 99.8\textsuperscript{th} percentile of L/(L'+L)_w saturations, ignoring the most extreme 0.2% of](image-url)
pixels in the hyperspectral image set. Image (i) is one of three scenes which contain
77.6% of the extreme pixels ignored in the denominator, represented by white in (ii). The
remaining 72 scenes included an average of 1611 extreme pixels, with a median of 52.
Image (iii) is representative of the scarcity of extreme chromaticities (iv) in the majority
of scenes.

2.3 Broadband uniform surfaces

In the following section we model the impact of the EnChroma filter on anomalous
trichromatic colour signals for spectrally broadband physical uniform surfaces.

2.3.1 Methods

Using our model of anomalous colour vision, we investigated the effect of a low-
transmission Cx25 EnChroma multi-notch filter on the chromatic signals available to
anomalous trichromats from uniform broadband stimuli. Responses to Stimulus Set 1 of
uniform Munsell surfaces (N=259) of equal lightness (Value=5) under LED illumination
(see Figure 8b) were modelled, with and without the EnChroma filter.

2.3.2 Results

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Table 1. The impact of the EnChroma filter on chromatic signals available from Dataset 1 of Munsell surfaces, presented as the change (conferred by EnChroma) in \( L/(L+L') \) as
a percentage of the $L/(L'+L)$ gamut, and change in $M'/(M+M')$ as a percentage of the $M'/(M+M')$ gamut – for details see Section 2.2.3.3.

Figure 5. Predicted chromatic signals available to (a; c) deuteranomalous and (b; d) protanomalous observers when viewing 259 Munsell surfaces without the EnChroma filter (black points) and with the filter (red points). The pair of chromaticities for each Munsell surface (with and without the EnChroma filter) are connected by a black line. Panels (a) and (b) show predictions of standard chromaticities in variants of the MacLeod-Boynton (1979) chromaticity diagram constructed for anomalous observers. Panels (c) and (d) show the same chromaticities relative to the white point (specified separately with and without the filter), which is the chromaticity diagram in which we typically express our results.

Figure 5 shows the changes in predicted cone-opponent signals conferred by the EnChroma multi-notch filter on the 259 Munsell surfaces. Figure 5 (a) shows, for the deuteranomalous trichromat, a systematic shift in chromaticities by EnChroma over increments in $L/(L'+L)$ and $S/(L'+L)$, suggesting that the lenses have a purple tint. Figure 5 (b) represents the impact of the EnChroma filter on the same Munsell surfaces for a protanomalous trichromat, with changes in chromaticity featuring a similar
systematic shift towards the \( M'/(M+M') \) decrement and \( S/(M+M') \) increment, suggesting a possible blue shift in colour appearance.

These observations of systematic hue shifts prompted us to adopt the strategy, outlined in Section 2.2.3.1, for quantifying the effect of the multi-notch filters independently of any systematic shift by calculating the chromaticities of surfaces with and without the multi-notch filters relative to their respective achromatic points. The achromatic points were defined as the chromaticity the ‘neutral’ 9.5 Munsell surface for all modelled conditions applied to the Munsell dataset. Results using this metric are shown in panels (c) and (d) of Figure 5 and are referred to as white point corrected, or \( L/(L+M)_w \). For both deuteranomalous and protanomalous observers, the EnChroma filters confer a change in chromaticity away from the centre of the chromaticity diagram. This represents an increase in cone opponent signals relative to the white point, which could result in a corresponding increase in perceived colour saturation. The increase in cone opponent signals is evident in all colour directions away from the white point, shifting both \( S/(L'+L) \) and \( L/(L'+L) \) in both incremental and decremental directions. Once exception to this generalized ‘expansion’ of the Munsell colour gamut was, for protanomals, \( M'/(M+M') \) decrements, where chromaticities with EnChroma (red points) are closer to the achromatic point than they are without EnChroma (black points).

When the impact of the filter on \( L/(L'+L) \) or \( M'/(M+M') \) signals are expressed as a proportion of the ‘chromatic gamut’ of natural scenes as defined in Section 2.2.3.3, the mean change in signal across all the stimuli in Dataset 1 is 5.84% for the deuteranomalous observer and 7.56% for the protanomalous observer, indicating an
overall increase in the saturation of the Munsell surfaces along anomalous trichromats’ ‘impaired’ colour dimension (Table 1). Considering the distribution of changes in predicted colour signals along these axes for all 259 Munsell surfaces, the maximum predicted increases were 20.51% for deuteranomals and 26.37% for protanomals. Despite the relatively modest mean predicted enhancements in colour signals across the set, for both protanomalous and deuteranomalous observers, 5% of the Munsell surfaces are predicted to gain a signal enhancement of over 15% of the anomalous L/(L+M) gamut.

To investigate whether the effect of the EnChroma filter is related to the saturation of the surface, a non-parametric correlation, Kendall’s Tau, was performed on the saturation of the unfiltered Munsell surfaces (absolute values of white point corrected L/(L+M)) and the signal change conferred by the EnChroma filter (∆(L/(L+M))) for the 259 Munsell surfaces of Dataset 1. The correlation indicated that L/(L+M) signal change conferred by EnChroma is significantly associated with starting saturation for both observers (r_{τ} = 0.276, p<.0001 for deuteranomals; r_{τ} = 0.648, p<.0001 for protanomals). This suggests that the enhancements conferred by the EnChroma filter correlated with the strength of the unfiltered signal.

A further Kendall’s Tau correlation revealed that the signal change conferred by EnChroma was significantly associated with the unfiltered L/(L+M) value, without white point correction (DA: r_{τ} =.877, p<.0001; PA: r_{τ} =.377, p<.0001). This suggests that signal enhancement from EnChroma filters increases with the redness of the surface.
2.4 Screen-rendered stimuli

In this section we model the impact of the EnChroma multi notch filter on the chromatic signals derived from stimuli rendered on RGB displays. The spectral power distributions of colours are considerably different when presented on RGB displays, which render RGB images with colours that are roughly metameric (for normal trichromats) to the colours of the real-world surfaces represented in the images. Since the spectra of the RGB primaries underlying display tristimulus values are relatively narrowband compared to the typically broadband spectra reflected from real-world objects, the action of multi-notch filters on light received from RGB displays is likely to be different from that received from the real-world surfaces that the colours in the scenes are metameric with. Given the spacing of the primaries, if the notches of the EnChroma filters coincide with the non-emissive regions of the display spectrum between the primaries we might expect the filters to have minimal impact on displayed colours.

2.4.1 Methods

To compare the effect of multi-notch filters on colours rendered on displays with their effect on the colours of real-world reflective surfaces, we modelled RGB display-rendered versions of the same Munsell surfaces as modelled in Section 2.3. We included 3 display types in the model: the cathode ray tube (CRT), for its prevalence in psychophysics research, the “in-plane switching” liquid-crystal display (IPS LCD) commonly used for mobile phone screens, and in widespread use in mid-range laptops and televisions, and light emitting diode backlit liquid-crystal display (LED LCD) used in high-end televisions, laptops and tablet devices. The SPDs of the RGB primaries were measured
using a Photoresearch PR655 SpectraScan spectroradiometer (Chatsworth, California USA), and are presented in Figure 6 for (a) a GDM-FW900 cathode ray tube (CRT) monitor (Sony, Tokyo, Japan), b) a DreamColor z27 (Hewlett Packard, Palo Alto, California USA) and (c) a 5th Generation iPad (Apple, Cupertino, California USA).

Spectra for colours metameric with a set of 40 Munsell surfaces of Value 5 and Chroma 8 under LED illumination were calculated for each display type (see Section 2.2.2.1).

Figure 6. SPDs of the three RGB primaries all at maximum intensity for each of the monitors included in the model; a) CRT monitor (grey), b) IPS LCD monitor (green) and c) LED LCD monitor (purple). Also shown on each panel is the transmission spectrum of the low transmission EnChroma filter and the spectral sensitivities of the L and L’ cones of the standard deuteranomalous trichromat.
2.4.2 Results

Figure 7. The predicted impacts of the EnChroma filter on the colour signals available to anomalous trichromats for stimuli rendered on RGB displays compared to physical surfaces. (a1-a3) Chromatic signals available to the deuteranomalous trichromat from 40 stimuli metameric with Munsell surfaces of constant lightness (Value=5) and saturation (Chroma=8) without EnChroma (black points), and with EnChroma rendered on (a1) a CRT monitor (grey circles), (a2) an IPS LCD monitor (green diamonds) and (a3) an LED-backlit LCD (purple squares). For comparison, the chromaticities of the same stimuli as physical surfaces with EnChroma (red circles, a1-3) are also provided. (b) The chromaticities represented in panels (a1-a3), plotted relative to an achromatic point (metameric with Munsell surface ‘Neutral 9.5’ viewed under the same LED illuminant as used to calculate the chromaticities of the plotted surfaces). Panel (c) represents the distributions of changes in the deuteranomalous $L/(L'+L)_w$ chromaticities for the whole of Dataset 2 of 259 Munsell surfaces (value=5) rendered on the same RGB displays. The metric used is as described in Section 2.2.3.3. The mean change in chromaticity is...
The predicted changes in deuteranomalous cone opponent signals due to the EnChroma filter for screen-rendered stimuli are shown in Figure 7. Panels (a1-a3) show the predicted changes in chromaticities for stimuli displayed on each monitor. Across all stimuli the greatest predicted signal enhancements with CRT monitors are half the size of those predicted for broadband surfaces (10.77% against 20.51% for deuteranomals, Table 2), with LED LCD monitors enabling slightly less and IPS LCD monitors enabling slightly more enhancement.

The predicted changes in deuteranomalous chromaticity conferred by EnChroma for stimuli displayed on the IPS LCD monitor (Figure 7, panel a2) are almost entirely confined to the \( L/(L'+L) \) axis, with minimal change in \( S/(L'+L) \). There are predicted shifts in \( L/(L'+L) \) on both sides of the achromatic point (panel b), resulting in a small but systematic gamut expansion along that axis. \( L/(L'+L) \) gamut expansion is present for stimuli rendered on all three monitors, but the gamut expansion predicted for the IPS LCD monitor is far smaller than that predicted for the other three monitors and the broadband Munsell surfaces. Predicted saturation enhancements for stimuli rendered on the CRT and LED LCD monitors match or exceed those predicted for the Munsell surfaces in the green region (\( L/(L'+L) \) decrements) but are much smaller than the enhancements predicted for Munsell surfaces in the red region (\( L/(L'+L) \) increments).
Table 2. The impact of the low transmission EnChroma filter on the chromatic signals available from Dataset 2 (screen-rendered Munsell surfaces), in comparison to Dataset 1 (physical Munsell surfaces, labelled ‘surface’). Changes in $L/(L'+L)$ conferred by EnChroma are presented as a percentage of the $L/(L'+L)$ gamut (see Section 2.2.3.3) and changes conferred in $M'/(M+M')$ as a percentage of the $M'/(M+M')$ gamut. Percentiles of the change in signal are given to indicate the distribution of signal change across the gamut, in which the 50th percentile indicates the median, and the 95th represents the highest signal change once the highest 5% are removed. The 0.1st and 99.9th percentile indicate the minimum and maximum ignoring the most extreme 0.2% of values.

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Table 3. ANOVA and post hoc tests comparing the impact of EnChroma on Munsell surfaces when viewed on different RGB monitors and as physical surfaces. Tests were run separately for deuteranomalous (grey tables) and protanomalous observers (yellow tables) with four levels of viewing mode: CRT monitor, IPS LCD monitor, LED LCD monitor, and physical surface. Post hoc Tukey tests indicate the significance of differences.
between each pair of viewing modes for deuteranomalous (grey table) and protanomalous observers (yellow table).

A larger maximum enhancement in \(L/(L'+L)\) is predicted for stimuli rendered on the LED LCD than for stimuli rendered on the other two monitors (Table 2), but there is also a greater predicted reduction in \(L/(L'+L)\) for some stimuli (Table 2).

Following the trend identified for broadband surfaces, the impact of the filters on anomalous \(L/(L+M)\) signals is predicted to be marginally stronger for protanomalous observers than for deuteranomalous observers (Table 2), but still much smaller than the signal enhancements predicted for broadband surfaces. Of the three monitors, the protanomalous signal enhancement from EnChroma is predicted to be greatest when stimuli are rendered on CRT monitors, whereas deuteranomalous signal enhancement from EnChroma is predicted to be greatest when stimuli are rendered on LED LCD monitors (Table 2).

The distribution of changes in deuteranomalous chromaticity conferred by EnChroma for a broader range of 259 Munsell surfaces (dataset 1) when rendered on the three monitors, is presented in Figure 7 (panel c). The ranges of predicted \(L/(L'+L)\) saturation enhancements are smaller for stimuli rendered on all three displays compared to those predicted for physical surfaces. The smallest range of predicted signal enhancements is for stimuli rendered on the IPS LCD monitor.

The predicted signal changes conferred by the EnChroma filters for each of the monitors and for physical surfaces were compared. One-way ANOVAs, with four levels (CRT, IPS LCD, LED LCD, and physical surface) were conducted separately for deuteranomalous \(\Delta(L/(L'+L))\) and protanomalous \(\Delta(M'/(M+M'))\) observers. The ANOVAs revealed a
significant impact of viewing mode for both deuteranomalous (F(3,1032)=12.107, p<.001***) and protanomalous observers (F(3,1032)=24.916, p<.001***). Post hoc Tukey tests revealed that the EnChroma filters are predicted to have a significantly smaller effect for stimuli rendered on any of the RGB monitors than for the physical surfaces, for both observers. The predicted signal changes did not differ significantly between the three types of RGB monitor, except for significantly greater predicted signal enhancements for the CRT monitor than the IPS LCD monitor for protanomals (p=.049*, Table 3).

In summary, although the filter is predicted to confer saturation enhancements for stimuli rendered on monitors, the predicted effects are weaker than for physical stimuli.

**2.5 Variation in illumination**

The following section investigates the impact of common illuminants on the effects of the multi-notch filters.

**2.5.1 Methods**

The spectral power distribution of the illuminant is expected to influence the impact of the EnChroma filter. To examine this, three common artificial illuminants and two natural illuminants were compared in the model. The artificial illuminants were light emitting diode (LED), halogen, fluorescent tube light (Philips TL-D). The spectrum of the LED and halogen illuminants were measured using a SpectraScan PR655 spectroradiometer (Photoresearch, Chatsworth, CA, USA) illuminating a standard polystyrene white standard (Sphere Optics, Uhldingen, Germany). The
spectrum of the fluorescent illuminant was obtained from an online dataset (Aphalo, 2015, mv.helsinki.fi) and converted from photon to energy. The two natural illuminants “Yellow daylight” and “Blue daylight” are two examples selected from the Granada daylights dataset (Hernández-Andrés et al., 2001).

2.5.2 Results
Figure 8. The impact of illumination on the effect of the EnChroma filter on deuteranomalous L/(L'+L) signals. Panel (a) The SPDs of the two natural illuminants: blue daylight (blue) and yellow daylight (chartreuse), against the transmission profile of the Low transmission EnChroma filter. Panel (b) The SPDs of the three artificial illuminants, LED (cyan), halogen (orange) and fluorescent TL-D (green) against the transmission profile of the EnChroma filter. Panels (c1-5) The changes in chromaticity of 40 Munsell surfaces (Value=5 Chroma=8) when viewed with each illuminant, c1: LED (blue circles), c2: Halogen (orange diamonds), c3: Yellow Daylight (chartreuse squares), c4: Blue Daylight (blue stars), c5: Fluorescent (green stars). Panel (d) Chromaticities of the 40 Munsell surfaces relative to a white point, viewed without the EnChroma filter (black points) and with the EnChroma filter (coloured points) under each illuminant. Panel (e) The distributions of signal changes for a broader dataset of 259 Munsell surfaces (Value=5), with median (red line), mean (black line) and standard deviation from the mean (black points).

Table 4. The impact of illumination on the effects of the EnChroma filter on the chromatic signals available from Dataset 1 of Munsell surfaces. Change in L/(L'+L) is presented as a percentage of the L/(L'+L) gamut and change in M'/(M+M') as a percentage of the M'/(M+M') gamut.

Table 4 shows the impact of illumination on the effects of the EnChroma filter on the chromatic signals available from Dataset 1 of Munsell surfaces. Change in L/(L'+L) is presented as a percentage of the L/(L'+L) gamut and change in M'/(M+M') as a percentage of the M'/(M+M') gamut.
point. For all illuminants an increase in saturation is predicted with the filter, revealed by chromaticities with the filter falling further from the achromatic point than without. Figure 8(e) and Table 4 show the distributions of predicted changes in $L/(L'+L)$ conferred by the filter for the broader set of 259 munsell surfaces of fixed lightness (Value=5), as a proportion of the $L/(L'+L)$ gamut (see Section 2.2.3.3). Median predicted changes in $L/(L'+L)$ caused by the filter are lower than the mean for all illuminants, suggesting a predominance of smaller enhancements in $L/(L'+L)$ saturation. For most illuminants, there are larger predicted enhancements in saturation for $L/(L'+L)$ increments (red hues), than for $L/(L'+L)$ decrements (green hues).
Table 5. Results of ANOVAs comparing the impact of the EnChroma filter under 5 illuminants, performed separately for deuteranomalous (grey table) and protanomalous observers (yellow table). P values from post-hoc Tukey tests are reported separately for each observer.

To test the impact of illumination on the effectiveness of the EnChroma filter, one way ANOVAs were performed with 5 levels for illumination, separately for deuteranomalous and protanomalous observers. The ANOVAs revealed a significant effect of illuminant for both deuteranomalous $L/(L'+L)$ signals ($F(4,1290)=4.145$, $p=.002^{**}$) and protanomalous $M'/(M+M')$ signals ($F(4,1290)=4.096, p=.003^{**}$). For the protanomalous observer the halogen is predicted to mediate the greatest signal enhancements by the filter, significantly greater than blue daylight ($p_{tukey}=.006^{**}$), and fluorescent ($p_{tukey}=.005^{**}$; Figure 8e and Tables 4 and 5). For the deuteranomalous observer, robust enhancements in $L/(L'+L)$ by the filter are predicted for all illuminants, though the fluorescent is predicted to mediate significantly weaker effects than LED ($p=.043^*$), blue daylight ($p=.009^{**}$) and yellow daylight ($p=.043^*$; Figure 8(e) and Tables 4 and 5). Signal changes predicted for the protanomalous observer are generally larger than those predicted for the deuteranomalous observer, but the deuteranomalous observer is predicted to receive greater enhancements at the 75th to 95th percentiles of signal change under blue daylight (Table 4).
2.6 Natural scenes
To predict effects of the filters on perception of real-life scenes, changes in chromaticity were calculated for hyperspectral images of natural scenes, which contain SPDs for each pixel.

2.6.1 Methods
To assess the expected impact of the multi-notch filters on colour perception of natural scenes, we used the model to predict the changes in $L/(L'+L)$ and $M'/(M'+M)$ for each of 50.93 million pixels from 75 hyperspectral images of natural scenes collected from 5 publicly accessible online datasets (Table 6).

<table>
<thead>
<tr>
<th>Abbreviation</th>
<th>Source</th>
<th>Number of scenes</th>
</tr>
</thead>
<tbody>
<tr>
<td>Párraga et al.</td>
<td>(Párraga et al., 1998)</td>
<td>29</td>
</tr>
<tr>
<td>Ruderman et al.</td>
<td>(Ruderman et al., 1998)</td>
<td>12</td>
</tr>
<tr>
<td>Nascimento et al.</td>
<td>(Nascimento et al., 2002)</td>
<td>8</td>
</tr>
<tr>
<td>Foster et al.</td>
<td>(Foster et al., 2006)</td>
<td>5</td>
</tr>
<tr>
<td>ICVL</td>
<td>(Arad &amp; Ben-Shahar, 2016)</td>
<td>21</td>
</tr>
</tbody>
</table>

Table 6. The sources of hyperspectral images of natural scenes used in Dataset 3. The scenes taken from the Arad & Ben-Shahar (2016) dataset, and Foster et al. (2006) dataset are a subset of the total databases.

For each hyperspectral scene, the spectral radiance was used, or reconstructed using the reflectance and illuminant spectra recorded at the time. The Nascimento et al. (2002) dataset contains spectral reflectances only, so an estimate of radiance was constructed using equal energy white as an illuminant. Three scenes were omitted from the Foster et al. (2006) dataset due to high levels of chromatic noise in pixels with low luminance.
This noise was present in other scenes in a low enough quantity that removing the pixels with the lowest 0.5% luminance values from the dataset sufficiently extracted the chromatic noise. Dataset 3 refers to all hyperspectral images combined, apart from instances where 4 examples are extracted from the dataset as representative examples: flora (N=1), man-made objects (N=2), and urban environment (N=1).

2.6.2 Results

Figure 9. Predicted chromatic signal changes by the EnChroma filter for individual hyperspectral scenes. Panel (a) Changes in deuteranomalous \( L/(L' + L) \) with EnChroma, panel (b) Changes in protanomalous \( M/(M + M') \) with EnChroma. Each individual hyperspectral scene is represented by a vertical line, with the dataset of origin indicated by colour: Ruderman et al. 1998 (orange), Parraga et al. 1998 (dark blue), ICVL (pale blue), Nascimento et al. 2006 (green), Foster et al. 2006 (purple). The range is indicated by the extent of the coloured line, and the 0.1, 5, 25, 50, 75, 95, and 99.9 percentiles are indicated by points.
Figure 10. Distribution of predicted changes in anomalous \( L/(L+M) \) signals for Dataset 3 conferred by the EnChroma filter, presented on a log scale (left) and a linear scale (right) for deuteranomalous \( L/(L'+L) \) signals (blue) and protanomalous \( M'/(M+M') \) signals (orange). Panel (a) includes the full range of predicted changes, and panel (b) has 0.1% of the most extreme predicted changes excluded from each end of the distribution for visual clarity.

The predicted changes in \( L/(L'+L) \) signals conferred by the EnChroma filter for 75 individual hyperspectral scenes are represented in Figure 9. Predicted changes across the scenes included in Dataset 3 are mainly positive, with median signal changes above zero for both deuteranomals and protanomals for all hyperspectral scenes (indicated by the 50th percentile of signal changes, Table 7). As for Munsell surfaces, (Sections 2.3 to 2.5), the EnChroma filter is predicted to confer a signal reduction for some samples, but a signal increase for the majority, with 89.63% of hyperspectral samples predicted to receive enhancement in \( L/(L'+L) \), compared to 85.33% of Munsell samples. For protanomalous observers 100% of the Munsell surfaces in dataset 1 were predicted to
receive signal enhancements, which reduced to 82.45% of samples for the hyperspectral dataset. The mean signal change per hyperspectral scene ranges from 0.45% to 9.47% for the deuteranomalous observer, and from 0.04% to 7.87% for the protanomalous observer (Table 7e). The greatest predicted mean enhancements are for scenes taken from the Parraga et al. database (1998), and the smallest predicted mean enhancements for scenes from the ICVL database (Arad & Ben-Shahar, 2016). Mean signal enhancements identified for Dataset 3 are generally lower than for Dataset 1.

Table 7. The predicted impact of the EnChroma filter on the chromatic signals available to anomalous trichromats from Dataset 3. The changes in chromaticity conferred as a percentage of gamut (see Section 2.2.3.3) are compared between Munsell surfaces and the natural scenes for the deuteranomalous observer (a), and the protanomalous observer (b). Four example hyperspectral images were selected to represent “flora” (N=1), “objects” (N=2) and “urban environs” (N=1) separated from the total dataset (“all”) of 75 natural...
scenes are compared for the deuteranomalous (c) and protanomalous (d) observers. e) Mean predicted signal changes per hyperspectral scene compared between origin datasets for deuteranomalous and protanomalous observers. The highest and lowest means are given (for individual images), in addition to the mean of all images included from that dataset, and standard deviations from the overall means are given.

The size of predicted signal changes for the Munsell surfaces of Dataset 1 was found to correlate with the saturations of the unfiltered surfaces (Section 2.3.2). To identify whether the same relationship is true for samples within hyperspectrally imaged scenes, a Kendall’s Tau correlation was run using the absolute $L/(L'+L)$ values from one hyperspectral scene (the example of “flora” in Figure 11), with the white point set as the mean chromaticity for the scene. A strong significant correlation was identified between the unfiltered saturation of samples within the hyperspectral scene and the signal change conferred by EnChroma ($r_\tau=.677 \; p<.0001$). This suggests that as with the surfaces from the Munsell dataset, the scale of the enhancement conferred by EnChroma is closely related to the unfiltered saturation. The impact of the relative scarcity of saturated chromaticities in natural scenes can be seen in the lower mean $\Delta L/(L'+L)$ for the hyperspectral dataset (2.17%) compared to Dataset 1 of Munsell surfaces (4.42%; Table 7a).

When presented on logarithmic scale (Figure 10, left), a small difference in the distributions of predicted signal changes is seen between protanomalous and deuteranomalous observers, with deuteranomalous observers predicted to benefit from a somewhat greater proportion of higher signal changes, and protanomalous observers predicted to receive a greater proportion of signal reductions.
Figure 11. The impact of the EnChroma filter on the $L/(L'+L)$ signals available in four example hyperspectrally imaged scenes. Row 1 (a1 to d1): The hyperspectral scenes presented as RGB images. Row 2 (a2 to d2): Heat maps showing predicted changes in $L/(L'+L)$ as a percentage of the gamut (Section 2.2.3.3), in which the hue represents the size of the predicted change in signal. Row 3 (a3 to d3): the full distribution of predicted $L/(L'+L)$ signal changes for each scene.

Figure 11 shows predicted signal changes for selected real-life visual environments. The greatest predicted signal enhancement was for scene containing flora (Figure 11 a1), with vegetation producing from a moderate predicted enhancement of 5 to 10%, and red flowers showing large, predicted enhancements of about 20% (Figure 11 a2). As for the flora, strong signal enhancements are predicted for manmade objects with saturated surface colours (panels b1 and c1 of Figure 11), particularly for reds. Panel (b2) shows that the strongest signal enhancements are modelled for the artificial flowers to the right of the scene, and in scene shown in panel (c2), the strongest enhancements are predicted for the red post to the left. The scene (panel c2) features a large area of predicted signal reduction for the clouded portions of the sky, a region of highly desaturated yellow. The
predicted signal contractions for other scenes are restricted to areas of low saturation, such as the white sections of the curb stone in the scene shown in panel (d2).

2.7 Filter variation

This section will assess how different EnChroma products affect the colour signals available to anomalous trichromats.

2.7.1 Methods

The spectral transmission profiles of 16 EnChroma filters were measured using a PR655 SpectraScan spectroradiometer (Photoresearch, Chatsworth, CA) for filters 1 to 4, and a PR650 SpectraScan spectroradiometer (Photoresearch, Chatsworth, CA) for filters 5 to 16. There was substantial variation in transmission profiles, which is predicted to have some impact on their function. The filters were sorted into three categories. The most common filter (66.7% of our sample) is the “low transmission filter”, which has been default filter in all other sections. The next most common filter is the “high transmission” filter, featuring a lower overall attenuation, a narrower notch in the 500nm region of the spectrum, but a similar notch to the “low transmission” filter in the 580nm region. The third class of filter is the “triple notch” filter as it features an additional notch around 640nm. One filter of each type was selected as an example with which to test the effect of filter type on the predicted impact of the filters on anomalous colour vision. Normalised transmission spectra of the three filters are shown in Figure 12a.
2.7.2 Results

Figure 12. The impact of filter type on predicted effect on anomalous colour vision. Panel (a) The transmission spectra of the three filter types against the normalised SPD of the LED illuminant used in this section. Panels (b1-b3) show the predicted colour signals available from 40 Munsell surfaces (Value=5, Chroma=8) when viewed without a filter (black points), and with the high transmission filter (b1; blue circles), the low transmission filter (b2; orange diamonds) and the triple notch filter (b3; chartreuse squares). Panel (c) represents the predicted changes in chromaticity of the Munsell surfaces for the 3 filters plotted with reference to the white point. Panel (d) shows the distributions of predicted signal changes for the hyperspectral dataset (N=50930062 pixels) as a percentage of the L/(L’+L) gamut (see Section 2.2.3.3). The Y axis has been truncated, with the 0.1st and
The impact of filter type on the predicted changes in chromatic signals for deuteranomalous observers for Munsell surfaces is represented in Figure 12. Despite substantial differences in the spectral transmission profiles of the three EnChroma filters (panel a), their predicted impacts on chromatic signals are similar. The most notable difference between the effects of the 3 filter types is in the direction of the systematic shift of the chromaticities (panels b1-b3). The low transmission filter (b2) is predicted to confer a shift mainly in the direction of $L/(L'+L)$ increments, while the “high transmission” (b1) and “triple notch” (b3) filters are predicted to cause substantial shifts in the direction of both $L/(L'+L)$ and $S/(L'+L)$ increments. Once plotted relative to a white-point (panel c), the rough equivalence in predicted $L/(L'+L)$ signal enhancements can be seen, in contrast to the predicted enhancements of $S/(L'+L)$ signal which are smaller for the high transmission filter. The distributions of predicted signal changes for the hyperspectral image dataset are shown in panel (d) of Figure 12 for deuteranomalous observers and summarized in Table 8 for both deuteranomalous and protanomalous observers.
Table 8. The impact of filter variation on the predicted changes in chromatic signals for Dataset 3 of hyperspectrally imaged natural scenes. Change in \(L/(L'+L)\) is presented as a percentage of the \(L/(L'+L)\) gamut and change in \(M/(M+M')\) as a percentage of the \(M/(M+M')\) gamut. Panel (c) Results of a two-way ANOVA to compare the predicted signal changes from three filters for two observers (deuteranomalous and protanomalous). There is a significant main effect of observer but not of filter, and no significant interaction.

To test the impact of variation in transmission profile on their effectiveness, three EnChroma filter examples were compared using a two-way ANOVA, with three levels for filter and two levels for observer (protanomalous and deuteranomalous). The ANOVA revealed a significant main effect of observer (\(F(2,1548)=37.672, p<.001^{***}\)), but no significant main effect of filter (Table 8c).

2.8 Variation between observers

The results discussed so far have used one ‘standard’ deuteranomalous observer and one standard protanomalous observer. The following section will predict the effects of the EnChroma filters on a greater variety of deutan and protan anomalous trichromats with
different cone sensitivity functions, in addition to protan and deutan dichromats, and normal trichromats.

2.8.1 Methods
In this section we examine the effectiveness of the EnChroma filter for a range of observers characterized by the different spectral separations between the peak sensitivities of the two X-linked cone types ($\Delta \lambda_{\text{max}}$). Thirteen observers were modelled: one normal trichromat with a $\Delta \lambda_{\text{max}}$ of 28.6 nm, five severities of protanomalous and deuteranomalous observer with $\Delta \lambda_{\text{max}}$ of 12, 9, 6, 3, and 1 nm, and two dichromatic observers, a deuteranope and a protanope, both with a $\Delta \lambda_{\text{max}}$ of zero. Cone fundamentals for these observers were by cone fundamentals created using a nomogram (see Section 2.2.2.4).
2.8.2 Results

Figure 13. The predicted effects of the EnChroma filter on the colour signals available to different observers: normal trichromats, deuteranopes, and six severities of deuteranomalous observer. (a) Cone sensitivity functions for the seven observers modelled: the S cone (blue), M cone (black), L cone (red), and five polymorphisms of L’ cone (shades of purple). Each phenotype is defined according to the $\Delta \lambda_{\text{max}}$ of the two X-linked cone types: normal trichromat (CVN): 28.6 nm, deuteranomalous (DA): 12 nm, 9 nm, 6 nm, 3 nm, 1 nm, and dichromat (DN): 0 nm. Panels (b1-5) show predicted chromaticities of 40 Munsell surfaces (Value=5, Chroma=8), when viewed without the filter (black points) and with the filter (coloured symbols) for five severities of...
predictions of the impact of variation in $\Delta \lambda_{\text{max}}$ on the effectiveness of the EnChroma filter are presented in Figure 13, with results for deuteranomalous observers presented in panels (b1-5) and panel (d), joined by a deuteranopic observer and the DeMarco et al. (1992) deuteranomalous observer used in other sections in panel (c). As the severity of anomalous trichromacy decreases with increasing $\Delta \lambda_{\text{max}}$, the systematic shift in chromaticity caused by EnChroma rotates towards the direction of $L/(L'+L)$ decrements (Figure 13, b1-b5).

EnChroma filters are not predicted to confer any enhancement of chromatic signals for dichromatic observers, as the notch filter works by increasing the functional difference between the two X-linked cone spectral sensitivities. In dichromacy there is only one X-linked cone, and so there are no $L/(L+M)$ signals to be enhanced (Figure 13c). The filters are therefore expected to have no ability to ameliorate the colour vision deficiency but may have some effect on the S/L or S/M dimension.
Table 9. Predicted effects of the low transmission EnChroma filter on the chromatic signals available for Dataset 3 of hyperspectral images for different observers. Eleven observers are compared, defined by the $\Delta\lambda_{\text{max}}$ of the X-linked cone sensitivities: the normal trichromat (CVN), and five severities of deuteranomaly (DA) and protanomaly (PA). Panel (a) Predicted changes in $L/(L'+L)$ are presented as a percentage of the $L/(L'+L)$ gamut for each severity of deuteranomaly (Section 2.2.3.3). Panel (b) Predicted changes in $M'/(M+M')$ are presented as a percentage of the $M'/(M+M')$ gamut for each severity of protanomaly. Panel (c) ANOVA comparing predicted signal changes for dataset 1 by EnChroma for 5 levels of anomalous trichromacy, comparing predicted signal changes that are not expressed as a proportion of the observer’s gamut, with separate tests performed for deuteranomaly (grey table) and protanomaly (yellow table). Panel (d) Post hoc Tukey tests detailing which comparisons differ significantly from each other. Panel (e) ANOVA comparing signal change from EnChroma for 5 levels of anomalous trichromacy, with signal presented as a proportion of the observer’s gamut, with separate tests performed on deuteranomaly (grey table) and protanomaly (yellow table).

For chromaticities specified relative to a white point (Figure 13c), the sizes of raw predicted saturation enhancements seem to be proportional to the severity of anomalous trichromacy with larger predicted enhancements for observers with a larger $\Delta\lambda_{\text{max}}$. To test
the impact of variation in $\Delta \lambda_{\text{max}}$ on the predicted signal changes conferred by the EnChroma filter, a one-way ANOVA was conducted with levels of 5 anomalous trichromacy. The test was performed separately for deuteranomaly and protanomaly, comparing the predicted changes in chromaticity of 259 Munsell surfaces under the default illuminant, LED, first with the signal change not expressed as a proportion of the observer gamut. The ANOVA revealed significant variation in the effect of the EnChroma filter with severity of anomalous trichromacy for both deuteranomaly ($F(4,1290)=21.92, p<.001$) and protanomaly ($F(4,1290)=41.12, p<.001$). Post hoc Tukey tests (Table 9, d) reveal that for deuteranomalous observers, differences between $\Delta \lambda_{\text{maxes}}$ need to be greater than 3 nm for the chromatic signals to significantly differ from one another (i.e., the signals available to the 12 nm and 9 nm are not significantly different, but observer contrasts featuring more than a 3 nm difference are). Deuteranomalous signals do differ significantly for some contrasts of 3 nm but not others (Table 9 d).

Once the change in colour signal is expressed as a proportion of the individual observer’s gamut, the difference between of observers the impacts of the EnChroma filter are not significant. Two one-way ANOVAs were conducted comparing $\Delta (L/(L'+L))$ or $\Delta (M'/(M'+M))$ as a proportion of gamut, with 5 levels of severity of anomalous trichromacy (Table 10e). The results showed no significant effect of severity of anomalous trichromacy, either for deuteranomaly ($F(4,1290)=1.523, p=.193$), or protanomaly ($F(4,1290)=.553, P=.697$). Although the difference in signal change between severities is not statistically significant, the impact of the filter has different trends between the deuteranomalous and protanomalous observers (Table 9a and b). For deuteranomalous observers, the impact of the filter tends to increase (signal reductions
get smaller and signal enhancements get bigger) as the severity increases. The opposite is true for protanomalous observers, the impact of the filter tends to decrease (signal reductions get bigger and signal enhancements get smaller) as the severity increases.

2.9 Luminance

2.9.1 Methods
EnChroma filters cause an overall reduction in light reaching the eye. In this section we calculate the expected attenuation in luminance. Luminance was calculated for each observer by summing the activities of the two X-linked cone cells (e.g. \( L+L' \) for deuteranomals and \( M+M' \) for protanomals). The luminance of stimuli attenuated by the EnChroma filter are presented as a percentage of the unfiltered luminance of the same stimuli, so that 100% indicates no reduction in luminance.

2.9.2 Results

Table 10. The impact of the EnChroma filter on the luminance of hyperspectral scenes. Panel (a) the mean transmission of each of the three filter types: low transmission, high
transmission, and triple notch. Panels (b-c) Luminance changes for all samples in dataset 3 for each of the three EnChroma filter types, with luminance presented as a percentage of original pixelwise luminance for: panel (b) the deuteranomalous observer, and panel (c) the protanomalous observer.

Figure 14. The predicted impact of the EnChroma filter on luminance (L+L’) available for four example hyperspectral scenes. Row 1 (panels a1 - d1): RGB images of the hyperspectrally imaged scenes containing a) flora, b) & c) manmade objects, and d) urban. Row 2 (panels a2 - d2): filtered luminance represented as a percentage of the unfiltered luminance for corresponding pixels, shown as a heat map. Row 3 (panels a3 - d3): Distributions of filtered luminance (over pixels) as a percentage of the pixelwise unfiltered luminance within each scene.

The predicted impacts of the EnChroma filter on the luminance of surfaces are presented in Figure 13 and Table 10, with the filtered (L’+L) presented as a percentage of original (L’+L) for corresponding pixels. All pixels show reduced luminance once filtered, compared to their unfiltered luminance. Table 10 (b) and (c) present the change in luminance for all samples in dataset 3, for the three EnChroma filter types. In comparison to the average transmission of the low transmission filter (37.57% transmission, Table 10, panel a), there is a greater reduction in luminance, with the luminance of
hyperspectral samples ranging from 12.27% of their unfiltered luminance at the greatest attenuation, to 40.50% of the lowest attenuation. Over 95% of samples from the hyperspectral dataset received a greater reduction in luminance than the neutral density equivalent of the EnChroma filter’s transmission level, indicated by the 95th percentiles of transmissions in Table 10b and c.

The high transmission EnChroma filter features a higher level of transmission, equivalent to a neutral density transmission of 57.7% (Table 10, a), and the resulting luminance of filtered hyperspectral samples are greater than those filtered by the low transmission EnChroma filter (Table 10, b and c). The “triple notch” EnChroma filter features the lowest transmission of the filters measured, due both to its lower transmission across the spectrum, plus an additional notch at ~640 nm (Figure 1) and has an overall transmission equivalent to a neutral density transmission of 26.89% (Table 10, a), but the majority of samples again receiving a greater reduction in luminance than predicted by the neutral density transmission.

Figure 14 presents the impact of the EnChroma low transmission filter on the luminance of four example for the deuteranomalous observer. Heat maps (panels a2 to d2) show that the highest luminance attenuation is found for desaturated colours, such as the concrete and sky shown in panel (b1), indicated by the heatmap in panel (b2). Colours with spectra containing a high proportion of light coinciding with a notch in the filter transmission spectrum feature high levels of attenuation, such as the yellow flower in panel (b1), which the heatmap in panel (b2) shows a greater reduction of luminance compared to the orange flower also pictured in panels (b1-2). The red flowers pictured in panel (a1) are not attenuated as much as the green foliage, which is reduced to ~27%
of its original luminance (panel a2), in comparison to the red flowers, which are \( \approx 32\% \)
of their unfiltered luminance (panel a2).

Plots showing the distributions of filtered luminance for the example scenes (Figure 14, panels a3 - d3) indicate that there are different ranges of luminance attenuation according to scene content. The highly chromatic scene containing flora (column a) produces a far greater range of luminance changes, compared to the generally desaturated urban scene (column d). The majority of pixels in all four scenes show a luminance that is a smaller proportion of the original luminance (\( \approx 27\% \)) than the mean transmission of the filter (\( \approx 37\% \)).

### 2.10 Discussion

EnChroma filters are designed to selectively attenuate light at particular wavelengths to increase the difference between the activities of the two X-linked cone classes in anomalous trichromacy. Our model predicted the impact of these filters on the cone-opponent signals available to the visual systems of anomalous trichromats, predominantly focusing on anomalous trichromats’ equivalent of normal trichromatic \( L/(L+M) \) signals, as this represents the dimension of vision that is impaired in protan and deutan colour vision deficiencies. The model predicts enhancements of colour saturation for the majority of samples from both uniform stimuli (dataset 1) and hyperspectral stimuli (dataset 3), for all the anomalous trichromatic observers modelled. The predicted changes to \( L/(L+M) \) saturation were overwhelmingly positive across all conditions examined,
implying a generalised enhancement in saturation by EnChroma filters. For the majority of conditions, reduction in L/(L+M) saturation was predicted for only a minority of samples.

EnChroma filters are predicted to be substantially less effective for stimuli rendered on RGB displays than for their metameric real-world surfaces. The mean predicted change in L/(L+M) saturation for Munsell surfaces rendered on displays is positive, but 29.8% to 47.8% smaller (depending on the display type) for deuteranomalous observers and 41.1% to 71.1% smaller for protanomalous observers than those predicted for physical surfaces under LED illumination. The SPD of the illuminant also impacts predicted saturation enhancements by the EnChroma filter, but more modestly than the impact of rendering stimuli on monitors. The effectiveness of the EnChroma filter is reduced by viewing conditions where there is reduced radiance in the spectral region of the primary notch (~580-600nm), for example, for stimuli rendered on IPS LCD monitors or viewed under fluorescent lighting.

The effects of the EnChroma filter on the chromaticities of natural scenes is smaller than their effect on the chromaticities of Munsell surfaces. For natural scenes there is a greater proportion of small predicted changes in L/(L+M) saturation than for Munsell surfaces, but the minimum and maximum predicted changes in L/(L+M) saturation are similar. The reduced predicted effects for natural scenes is likely attributable the greater prevalence of desaturated surfaces, as there is a strong correlation between the predicted change in L/(L+M) saturation with EnChroma and unfiltered saturation. There are some differences in the predicted effectiveness of EnChroma between individual scenes: scenes
containing flora and other very saturated surfaces produce larger predicted changes in L/(L+M) saturation. The differences in predicted effectiveness for individual scenes also leads to some differences in predicted effectiveness between hyperspectral datasets. The dataset producing the largest predicted saturation enhancements is that of Parraga et al. (1998) which contains autuminal scenes of foliage. The Arad and Ben-Shahar (2016) dataset (ICVL) depicts arid landscapes and urban scenes with very desaturated chromaticities for which smaller enhancements of saturation are predicted.

Variation in filter transmission profile was found to have only a small effect on predicted changes in L/(L+M) saturation despite the notable differences between filter types in secondary notch width (at ~480-500nm), notch depth, and number of notches. The core function of the filters appears to be tied to the primary notch at ~580nm-600nm, which is present in all 3 filters modelled.

The severity of anomalous trichromacy has an impact on the predicted changes in L/(L+M) saturation conferred by the EnChroma filter. The raw size of predicted changes is smaller the smaller the $\Delta \lambda_{\text{max}}$ of the X-linked cone sensitivities. However, when the change in signal is scaled as a percentage of the individual observer’s colour gamut, the difference between severities is minimal, meaning that different observers are predicted to receive a similar percentage enhancement of L/(L+M) saturation from the filters. The protanomalous observers modelled using Stockman & Sharpe (2000) fundamentals with a nomogram to simulate five severities of protanomaly were predicted to receive the smallest benefit from EnChroma filters. The protanomalous observer represented by a combination of Smith & Pokorny (1975) and DeMarco et al. (1992) cone sensitivities
was predicted to receive strong enhancements, indicating that the effectiveness of EnChroma depends on the precise sensitivities of the X-linked cone classes.

The findings of this investigation mark a departure from the consensus in existing literature that the EnChroma filters are ineffective. However, our findings are not in direct conflict with existing research where the approaches used may have led to a failure to identify the effects. The investigation by Gomes-Robledo et al. (2018) was compromised by the modelling approach used and is not expected to provide an accurate estimation of the EnChroma filter’s effect. Investigations identifying the effect of EnChroma filters on the outcome of CVD tests have generally found little (Pattie et al., 2017) or no effect (Almutairi et al., 2017; Mastey et al., 2016), but these may not be incompatible with our positive findings. The broad net predicted enhancements of saturation by the EnChroma filters may not provide enough additional signal to pass certain CVD tests, yet still confer meaningful enhancement to colour perception in everyday life. Additionally, any changes in colour perception of diagnostic tests for CVD by the EnChroma filters will depend on the interaction between the filter’s transmission spectrum and the light reflected from the tests. For example, our model predicts that the effect of the filters is reduced for chromaticities viewed on screens, which could help explain the limited observed effects of the filters on performance on tests for CVD presented on screens, such as the ColorDX test (Almutairi et al., 2017). For the FM100 Hue test, the EnChroma filters have been found to produce a rotation in the axis of errors for anomalous trichromats (Pattie et al., 2022) which may relate to the systematic hue shifts identified in this paper (Figure 5, a and b).
The findings of this investigation indicate that there are enhancements in the chromatic signals available to anomalous trichromats with the EnChroma filters but does not give indication of whether the predicted changes in cone-opponent signals are of a size to be useable by the visual system, and to therefore result in changes in colour perception. The ability of the visual system to use the predicted signal changes for perception is the focus of behavioural experiments in an accompanying paper (Chapter 3).
Chapter 3: The effect of multi-notch filters on the colour perception of anomalous trichromats

3.0 Abstract
Notch filters are marketed as wearable aids for colour vision enhancement for people with colour vision deficiency, despite a lack of scientific evidence supporting their effectiveness. In our companion paper (Chapter 2), we have shown, using a physiologically accurate model of anomalous colour vision, that multi-notch filters manufactured by EnChroma Inc. are predicted to confer an enhancement to cone opponent signals for anomalous trichromatic observers.

To determine whether this predicted enhancement in colour contrast signals leads to a measurable difference in colour perception, we conducted a battery of behavioural tests of colour perception with deuteranomalous observers. We investigated the impact of the EnChroma filters on detection thresholds, colour matching, and subjective ratings of perceptual dissimilarity. Our findings support the model’s predictions suprathreshold, where we found changes in colour appearance using a colour matching task that approximated the scale of enhancements predicted by the model for both the L/(L+M) and S/(L+M) subsystems. However, we observed a reduction in detection thresholds only for red surfaces, replicating only the largest predictions of the model. Perceptual ‘colour spaces’ for stimuli reconstructed via multidimensional scaling from dissimilarity ratings showed significant enhancement for the L/(L+M) subsystem before habituation but not after habituation to the filters.
3.1 Introduction

3.1.1 EnChroma

EnChroma glasses are aids designed to enhance the colour vision of individuals with anomalous trichromatic colour vision deficiency (CVD). An enhancement of chromatic contrast is provided by notches in the filter transmission spectrum, spectrally positioned to coincide with the difference in the peak sensitivities of the L-type and M-type cones, to increase the difference between their activities when exposed to broadband colored light.

Since EnChroma glasses were brought to market in 2012, the design of the filters has undergone a series of modifications. In their first few years of trading, EnChroma produced aids for both normal trichromatic observers and anomalous trichromats (c.2012-2015), later reducing the range to one filter for all anomalous trichromats but at three broad levels of light attenuation (Cx-15, Cx-25, Cx-65, c.2015-2017). Presently, EnChroma offer two attenuation levels (Cx1 indoor, Cx3 Sun), and one product designed specifically for strong protanomals (Cx3 Sun SP, c.2017-present; www.enchroma.com).

EnChroma has gained considerable attention in mainstream and social media, and despite intermittently carrying disclaimers confirming that the aids are “not a cure for color-blindness” and are “not designed to improve scores on color-blindness tests” the website also hosts articles describing the product as a “cure”, alongside language and visualizations that suggest that this is the case (www.enchroma.com, 2017, accessed via archive.org). There is a need for scientific research to investigate the effects of multi-notch filters on anomalous colour perception, and specifically to test the claims made by
EnChroma in marketing their products. In the present study, we test two aspects of colour perception: discrimination, and colour appearance, to assess the perceptual effects of EnChroma filters in comparison with predictions from our physiologically accurate model.

### 3.1.2 Anomalous trichromacy

Normal human colour vision is based on a comparison between the signals of three classes of retinal cone sensitive to short (S), medium (M) and long (L) wavelengths of light. Colour vision is thought to be based on signals from two postreceptoral subsystems which compare cone signals: the ancestral S/(L+M) subsystem compares signals from the S cones with combined signals from the L and M cones allowing colour discrimination along a violet-chartreuse axis (Mollon, Estévez, et al., 1990). The more recently evolved L/(L+M) subsystem compares the signals from the L cone class with those from M cones, allowing discrimination along a teal-cherry colour axis (Mollon, Estévez, et al., 1990), often paraphrased as ‘red/green’. The majority of colour vision deficiencies (CVDs) arise from polymorphisms in the opsin genes that encode the L and M cone opsins. Anomalous trichromacy is a mild form of CVD in which one cone class inputting to the L/(L+M) subsystem is replaced by an anomalous cone class containing a photopigment with a spectral sensitivity that is much more similar to that of the other X-linked cone class than in normal trichromacy. The strength of the L/(L+M) cone opponent signal is dependent on the difference between the spectral sensitivities of two cone classes. Red-green discrimination in normal colour vision is enabled by a roughly 27 nm spectral separation between the peak sensitivities of the L and M cones, while
anomalous trichromats can present many variants of anomalous opsin, resulting in cone spectral separations varying between 12 nm and 3 nm or smaller (Bosten, 2019; J. Neitz & Neitz, 2011).

3.1.3 Existing Research
Much of the existing research testing the effectiveness of notch filters as an intervention for CVD has focused on identifying the impact on outcomes of diagnostic tests for CVD, with the exception of Gomez-Robledo et al. (2018), who used a predictive modelling approach combined with a behavioural colour naming task, and Werner et al. (2020) who used MLDS to identify changes in chromatic sensitivity after use of the filters. Mastey et al. (2016) and Patterson (2017) tested the effect of the EnChroma glasses on performance on the CAD test (Barbur & Rodriguez-Carmona, 2017) a digital diagnostic test for CVD which measures colour discrimination thresholds around the hue circle to identify the colour axes of maximum and minimum sensitivity. Both Mastey et al. (2016), who tested 10 deuteranopes (DNs), 8 deuteranos (DAs), and 9 protanopes (PNs), and Patterson (2017) who tested 7 DNs, 6 DAs, 1 PN and 1 protanomal (PA), found that the EnChroma glasses did not significantly improve red-green discrimination thresholds on the CAD test. Both papers concluded that their findings do not support the claims made by EnChroma. Alvaro et al. (2022) examined the effect of the EnChroma filter on the discrimination thresholds of 16 CVD observers (including 4 PAs, 4DAs, 4 DNs and 4 PNs) using the CVA-UMinho colour discrimination test (CVA-UMinho, Colour Science Lab, Centre of Physics, University of Minho, Portugal), similar to the
CAD test and the Cambridge colour test and identified no significant change in CVD discrimination thresholds with an EnChroma filter.

Almutairi et al., (2017) tested the effect of EnChroma filters on performance on the Color DX test (a computerized version of Ishihara test, Waggoner Diagnostics, Arkansas USA) and the X-Rite test (a computerized version of the FM100 test, X-Rite Pantone, Michigan USA) alongside that of unbranded red filters and green filters on a small sample of 6 severe deutans, 2 moderate deutans and 2 severe protans. They found that there was no significant improvement in the results of the online FM100, however, there was sufficient improvement in the Color Dx to raise two of the participants from severe to moderate classifications (one protan, one deutan). A significant reduction in Ishihara test error rate was also identified on testing carried out with 16 CVD observers (Álvaro et al., 2022), including a protanomal who became reclassified as “mild” with the EnChroma filter after being classified as a “strong” protan without the filter.

Kitchens and Cisarik (2017) and Pattie et al., (2017) tested the effectiveness of the EnChroma glasses using the physical FM100 test. Pattie et al. (2017) collected data from 118 participants (Normal trichromat control (C)=24, DA=30, Extreme Deuteranomalous (eDA)=12, DN=9, PA=15, Extreme Protanomalous (ePA)=5, PN=20), and found significant reductions in error scores (Z=-2.611 p<0.01), confusion index (for deutans; Z=-3.329 p<0.005), an increase in selectivity index for protans (Z=-4.719 p<0.001), and a significant shift in the deutan confusion axis towards the protan confusion axis (Z=-5.168 p<0.0001). Their findings need to be interpreted in the light of significant practice effects found among the controls (Z=-1.988 p<0.05). Kitchens and Cisarik (2017) found
a significant reduction in errors for FM100 colour discriminations in the blue region (FM100 caps 22-42), from 12 CVD participants (of undisclosed category), and an increase in errors in the yellow-green region (FM100 caps 43-63). The total mean error score for CVD participants was not significantly different between the EnChroma filter and a neutral density control filter. Another investigation using the FM100 Hue test (Álvaro et al., 2022) observed a change in the angles of colour confusion axes in a group of 16 CVD observers (4 DAs, PAs, PNs and DNs) but concluded the overall impact of the EnChroma filter was not significant.

Gomez-Robledo et al., (2018) tested the impact of EnChroma filters on the outcome of the FM100 hue CVD diagnostic test (Farnsworth, 1943b), and on a colour naming task using surfaces from the X-Rite Color Chart (X-Rite Pantone, Michigan USA). They found that the deutan confusion line shifted towards the protan confusion line, replicating findings by Kitchens et al. (2017) and Pattie et al. (2017), suggesting a systematic alteration in colour perception but not necessarily an increase in sensitivity.

Werner et al., (2020) identified a perceptual learning effect following use of EnChroma filters, where luminance and chromatic contrast was increased from baseline after two weeks of using the filters, measured without the filters. These changes were found in anomalous trichromats but not normal trichromats. This finding suggests a plastic adaptive response to temporarily increased chromatic signals in those with previously restricted colour signals.

Limitations to studies carried out so far, aside from the research done by Pattie et al. (2017), included limited sample sizes and a disproportionate number of dichromatic
Alvaro et al., (2022) tested equal numbers of anomalous trichromats and dichromats and despite reporting significant difference between observer types, grouped their findings into one CVD category. The rationale for this conglomeration was the filter’s potential introduction of luminance differences providing novel information for dichromatic observers, enabling the breaking of some pseudoisochromatic pairings. However, few of the tests they conducted are thought to rely on luminance signals. Since the core functionality of the EnChroma filter is dependent on enhancing the difference between the two cone signals within the L/(L+M) subsystem, they are not expected to be effective for dichromats (Chapter 2, www.EnChroma.com, 2018).

3.1.4 Other ‘treatments’ for CVD
EnChroma Inc. was not the first to design optical filters to enhance anomalous colour vision: there have been a selection of products brought to market over the last 50 years. The majority of these are either interocular bandpass filters, designed to improve the ability to discriminate colour by using interocular lustre induced by unequal luminance attenuation between the two eyes, or binocular bandpass filters, designed to increase the signals sent by the anomalous and normal L or M-type cones.

Intraocularly discrepant bandpass filters were first marketed by Zeltzer as the X-Chrom filter (Ipswich, Massachusetts USA; Zeltzer, 1991), then by Harris as the Chromagen filter (Birkenhead, United Kingdom; Harris, 1999), then by Azman as the Colormax filter (Birmingham, Alabama USA; Muttaqin & Suwandi, 2011). The lenses were advertised as being effective for both dichromats and anomalous trichromats. The majority of research testing intraocularly discrepant bandpass filters has examined their impacts on
colour vision solely through their effect on performance on diagnostic tests for CVD. Studies have used the Ishihara Plates test (Paulson, 1980; Swarbrick et al., 2001; Welsh et al., 1978), the FM100 (Kassar et al., 1984; Matsumoto et al., 1983), the D-15 Panel test (Paulson, 1980; Swarbrick et al., 2001) the Lantern test (Kassar et al., 1984; Paulson, 1980; Swarbrick et al., 2001), and the Hardy Rand Rittler (Paulson, 1980; Welsh et al., 1978) to investigate the effectiveness of these filter types. Results show universally that the lenses improve scores on tests. This ‘enhanced’ performance is likely based on induced luminance differences between confusion colours (e.g., for the Ishihara Plates test and the HRR) through color-selective attenuation, which then causes a difference in interocular lustre between confusion colours. The use of interocular bandpass filters has not been found to result in any significant improvement on tasks involving colour arrangement (e.g., the FM100 and the Panel D-15), presumably because interocular lustre does not provide a reliable signal for colour appearance. Performance changes on diagnostic tests for CVD do not necessarily constitute an improvement in colour vision, if they simply break metamerism between the figure and ground or are based on signals from interocular lustre rather than ‘colour’ signals (Hartenbaum & Stack, 1997; Sharpe & Jagle, 1999; Siegel, 1981).

Colorlite Kft. (Halásztelek, Hungary) produce wearable filters developed by Abraham and Wenzel using a rationale similar to that of EnChroma (Abraham et al., 1995), in that a change in spectral sensitivity is induced by attenuating one portion of the spectrum. For Colorlite (originally named Coloryte) filters, the attenuation profile is built up using subtractive mixes of multiple dyes, rather than by employing a fixed notch. The Colorlite product is designed to be specific to each type of anomalous trichromacy, tailoring filter
attenuation profiles for each case. A patent was granted with no limit on the variations of dye combinations to be used in the product (Abraham et al., 1995). Publications which have not been peer-reviewed (www.colorlitelens.com/publication) suggest that some Colorlite filters enhance the colour perception of dichromatic observers, though evidence of this has not been provided.

The first aids to use a spectral notch included the EnChroma and Oxy-Iso filters. In their early stages these two products were developed in partnership, but later diverged in purpose. Changizi’s Oxy-Iso product (Vino Optics, U.S. Virgin Islands, Barber & Changizi 2012) was developed for medical contexts, as a means of enhancing perception of blood volume and blood oxygenation levels for normal trichromats (www.vino.vi, 2020). Several methods for the construction of notch-filter lenses have been developed by Badawy et al., (2018) using dyes, and others (Karepov & Ellenbogen, 2020) using gold nanostructures. Both are at a prototype stage and are described in greater depth in Chapter 2.

3.1.5 Rationale
We present three experiments to test the effect of EnChroma multi-notch filters on the colour perception of 10 deuteranomalous observers. Suprathreshold colour appearance was examined with an asymmetric matching task, sensitivity at threshold was examined with a 4AFC discrimination task, and internal representations of colour were assessed using multidimensional scaling applied to the results of a colour difference rating task.
The selection of stimuli was guided by the physiologically accurate model of colour vision presented in Chapter 2, which predicted the changes in colour signals available to the cone opponent channels $L/(L+M)$ and $S/(L+M)$ conferred by the EnChroma filter. The model predicted that chromatic signal enhancements would be substantially smaller for narrowband stimuli such as those produced by RGB screens than for broadband stimuli. The three experiments presented here were therefore carried out using only broadband surface stimuli.

The experiments were carried out at 2 time points to explore the effect of habituation, following EnChroma’s advice to customers that for “optimal effectiveness, wear the lens for at least 10 hours in a variety of situations over the course of 1-2 weeks” (EnChroma User Manual and Warranty, 2017). After the three experiments were completed at time point 1, participants were loaned a pair of EnChroma glasses and asked to wear them for a minimum of 10 hours before taking part in the second experimental session at time point 2.

3.2 Overview of experiments and hypotheses

3.2.0 The Model
The model presented in Chapter 2 has informed the selection of stimuli used throughout this study and provides predictions for how the chromatic signals available to the visual system are altered by the filter being tested. The model predicts changes in chromatic signals for any given surface reflectance (Figure 1, b) under any illuminant (a) attenuated by any given filter (c), resulting in predicted cone responses to light at each wavelength.
(d) for any given observer. For the current study the L, M and S cone sensitivity functions
of the normal trichromatic (CVN) observer were replaced with sensitivity functions for
the L, L’ and S cones of deuteranomals, where the L an S cone fundamentals were those
published by Smith and Pokorny (1975) and the L’ cone fundamental was that published
by DeMarco et al. (1992). The cone responses to light at each wavelength are summed
to give overall cone activities in response to the light reaching the eye (e). Retinogeniculate cone-opponent signals are then estimated as MacLeod Boynton (1979)
chromaticity coordinates, which for the CVN observer are S/(L+M) and L/(L+M), but
for the deuteranomaly are substituted with S/(L’+L) and L/(L’+L) (f).

Figure 1. Step by step depiction of the model used to calculate the impact of notch filters
on the observer-specific chromaticities of surfaces. The spectral energy reflected from the
surface is calculated as the product of the illuminant spectrum (a) and the reflectance spectrum of the surface being viewed (b). These combined, form the radiance spectrum, which is attenuated by the transmission spectrum of the notch filter (c) as the light passes through the EnChroma glasses. The responses to each wavelength of light of the cones are calculated using cone sensitivity functions for the anomalous observer (d). Cone responses at each wavelength are then summed to estimate the activities of the three cone classes (e). These are then plotted in a variant of the MacLeod Boynton (1979) chromaticity diagram (f) constructed for deuteranomals.

3.2.1 Experiment 1: Colour matching task
To measure the impact of the EnChroma filter on suprathreshold colour appearance, deuteranomalous observers were asked to complete a colour matching task. A coloured target was presented under one filter (either the EnChroma filter or a control neutral density filter), and an array of coloured surfaces was presented under the other filter. The observer’s match between the target and a surface from the array will reveal any changes in perceived hue and saturations conferred by the EnChroma filter. The model predicted that when presented to a deuteranomalous observer under an LED illuminant, cone-opponent colour signals from target surfaces would be enhanced by the EnChroma filter (Figure 2). If the visual system is able to make use of these increased signals, there could be an increase in perceived saturation. If this is the case, a target surface viewed through the EnChroma filter should appear more saturated, and therefore the match selected from the matching array viewed under the control filter should be of a higher saturation than it would be if both the target and matching array were viewed under the same filter. The effect was also tested in the opposite direction, with the target presented under the control neutral density filter and the match selected from an array of coloured surfaces presented under the EnChroma filter. Here, the model predicts that a less
saturated surface will be selected (because the perceived saturations of colours in the matching array are predicted to be enhanced). To this end, the task was conducted in two stages to allow a reversal of the filters, one in which targets were viewed under the control filter and matches selected from the array of surfaces viewed through the EnChroma filter, and a stage with these reversed where targets were viewed under the EnChroma filter and matches selected from an array of surfaces viewed under the control filter.

Figure 2. The subset of Munsell surfaces with Value 5 \((N=259)\) plotted in a variant of the MacLeod Boynton (1979) chromaticity diagram for the deuteranomalous observer. The chromaticities of the surfaces viewed under the EnChroma filter (red points) are plotted, and under the control filter (black points), connected by a black line. (a) ‘Raw’ chromaticities, where surfaces viewed under EnChroma show an overall shift in the red direction. (b) The same data plotted relative to an achromatic point, revealing that the chromaticities of surfaces under EnChroma fall further from the achromatic point than under the control filter (an increase in cone-opponent signals).
3.2.2 Experiment 2: Discrimination task
If the increase in cone opponent signals with the EnChroma filter predicted by the model is useable by the visual system, this should result in reduced colour discrimination thresholds. To test whether the predicted enhancements in colour signals are sufficient to reduce discrimination thresholds, a 4AFC discrimination task was conducted where observers viewed stimuli through the EnChroma filter and a control neutral density filter in different conditions. Since our model predicted that the EnChroma filter should confer increases in cone-opponent colour signals in all colour directions when surfaces are illuminated by an LED source (Figure 2), we predicted that colour discrimination thresholds should reduce when stimuli are viewed through the EnChroma filter compared to the control filter.

3.2.3 Experiment 3: Dissimilarity task
Our model predicted that under illuminants with lower radiance at shorter wavelengths, the EnChroma filter will confer smaller signal enhancements in \( S/(L'+L) \) than in \( L/(L'+L) \). If the visual system is able to make use of the changes in cone opponent signals, we might expect perceived colour differences to be enhanced to a greater degree along the \( L/(L'+L) \) dimension than along the \( S/(L'+L) \) dimension of the MacLeod Boynton (1979) chromaticity diagram. Multidimensional scaling is a method that can be used to convert numerical difference ratings into Euclidean distances between the set of stimuli rated. For ratings of the perceived differences between a set of colours, colours described as similar will have smaller distances between them in the MDS solution, and colours rated as more different will have greater distances between them in the MDS solution. Since the stimuli are rated \( \textit{in relation} \) to one another, colour enhancements that
affect all colour axes equally may not be evident in MDS solutions as they would not alter the *relative* perceived differences between different pairs of stimuli within the set. However, as our model predicts unequal colour enhancements for the $S/(L+M)$ and $L/(L+M)$ subsystems for halogen lighting, MDS solutions are expected to be selectively extended along the axis with greater enhancement of perceived colour signals.

To investigate any changes conferred by the EnChroma filter on the representation of a set of colours, dissimilarity ratings were collected for 13 Munsell surfaces with constant Value but varying Hue and Chroma, displayed pairwise under a halogen illuminant. We used multidimensional scaling (MDS) to reconstruct perceptual ‘color spaces’ from a matrix of dissimilarity ratings. We expected that if the signal enhancements predicted by the model confer changes in colour appearance along the $L/(L+M)$ axis more than along the $S/(L+M)$ axis, then there would be a selective expansion in the MDS-reconstructed colour spaces along the stimulus axis aligned with $L/(L+M)$.

### 3.3 General Methods

#### 3.3.1 Participants
A total of 10 male participants (mean age 26) were recruited at the University of Sussex campus. Recruitment was in person on campus by screening for CVD among the general population ($n=773$), which was via either the Ishihara Plates Test (Ishihara, 1917), or via a shortened diagnostic procedure using an Anomaloscope (Oculus; Wetzlar, Germany). The shortened anomaloscope procedure consisted of 3 trials in which the participant was asked to find a colour match but to ignore luminance or brightness difference, using
only one of the two dials. Participants were asked to “turn the dial until the colours match”. The starting position of the trials alternated between the two extremes of the normal matching range. If a participant accepted any matches outside the normal range, a full anomaloscope procedure was carried out.

The colour vision of all those taking part in the study was characterised through the full anomaloscope procedure, which consisted of five matches, adjusting both hue and luminance. Participants were excluded from the study if their colour vision was found to be normal trichromatic (n=4), deuteranopic (n=12), extreme deuteranomalous (n=14), protanopic (n=8), protanomalous (n=12), or extreme protanomalous (n=5) during the second anomaloscope session. The individuals found to have deuteranomalous (n=37) colour vision were invited to take part in the study. Individuals who had previously used EnChroma products were excluded from participating in the study (N=3) as it had not yet been determined whether adaptation would affect the impact of the filters. Of the remaining 37 deuteranomals, 10 chose to take part in the study.

The study received ethical approval from the Science and Technology Cross-Schools Ethics Committee (C-REC) at the University of Sussex (ER/LS487/4).

3.3.2 Filters
The EnChroma filter used in all experiments was the Cx-25 filter selected as a representative example of the most common filter profile from a range of 16 EnChroma products measured between 2017 and 2018 (See Chapter 2 for details). This filter was designed for both indoor and outdoor use, so was suited the illumination levels achievable
in the testing environment, and in our model this filter outperformed the filter advised for exclusive indoor use in the predicted enhancements to colour perception conferred.

A neutral density filter (Lee Filters, Hampshire, UK) of 0.6 log unit attenuation was used as a control filter, to match the attenuation of the EnChroma filter. The transmission profiles of the control and EnChroma filters (Figure 3a) were measured using a spectrophotometer (PR650 SpectraScan, PhotoResearch, Chatsworth, CA in reference to a stable white surface (polytetrafluoroethylene, Sphere Optics, Uhldingen, Germany) under LED illuminant.

![Figure 3](image)

*Figure 3. Transmissions of filters, spectral power distributions of illuminants and chromaticities of stimuli used in the experiments. (a) The transmission spectra of the EnChroma filter (Cx-25 Explorer) and the control filter (Neutral density, ND, Lee filter). (b) The normalized spectral power distributions of the two illuminants used, LED and Halogen. (c) Chromaticities of all stimuli used in the three experiments under the LED illuminant, including the subset of the Munsell dataset with a value of 5 (black points), the stimuli used in the Discrimination task (blue circles), the stimuli used in the Rating task (pink circles) and the targets used in the Matching task (yellow circles).*
3.3.3 Illuminants
A white light-emitting-diode (LED) illuminant was used for Experiments 1 (color matching task) and 2 (color discrimination task) since the model predicted strong signal enhancements for both cone opponent subsystems (Figure 1a). For Experiment 3 (rating task) a halogen illuminant was used, to produce predicted signal enhancements that were unequal between the two cone-opponent subsystems. Our model predicted that the EnChroma filter would confer greater signal enhancements in the L/(L+M) subsystem in conjunction with a halogen illuminant than in conjunction with other broadband illuminants, while not substantially affecting S/(L+M) signals (Chapter 2, Section 2.5).

The illuminant was suspended 56 cm from the viewing surfaces and illumination was restricted to the inside of the viewing box. Environmental lighting was minimal, with scotopic light levels outside the viewing apparatus, and low levels of the experimental illumination escaping the top of the apparatus.

3.3.4 Stimuli
The predicted effects of EnChroma on all stimuli used in the experiments were modelled prior to testing (Sections 3.4.1, 3.5.1 and 3.6.1). Stimuli used in Experiment 1 (colour matching, Figure 3c, yellow points) and Experiment 3 (rating task, Figure 3c, pink points) were samples from the Munsell colour atlas (Glossy edition, Pantone, Michigan USA) of Value 5 (Figure 3c, black points). The spectra were obtained from an online-accessible dataset of 1600 Glossy Munsell surface reflectances provided by the University of Eastern Finland (Orava, https://sites.uef.fi/spectral) at a resolution of 1 nm for the range 380 nm to 780 nm.
The stimuli used in Experiment 2 (discrimination task) were custom-made 4AFC stimuli presenting three white surfaces and one chromatic surface per trial. Eighteen stimuli per hue direction were used to conduct a staircase procedure. The saturation of the chromatic target increased monotonically in seven hue directions (Figure 3c, blue circles). The stimuli were custom-made black acetate frames with four square windows (4 cm² each), containing four painted uniform surfaces. Within each frame, three surfaces were achromatic acrylic white, and one target surface was painted with acrylic white mixed with differing quantities of chromatic acrylic paint. Chromatic surfaces were painted, and measured using a PR655 spectrophotometer (Photoresearch, Chatsworth, CA), under LED illumination, in reference to a polytetrafluoroethylene white standard (Sphere Optics, Uhldingen, Germany). Eighteen samples were selected to form the monotonic saturation scale for each of seven hue axes tested (plotted in Figure 1c).

3.3.5 Apparatus
All experiments were carried out using a custom viewing box (Figure 4), designed to be adjustable to allow the configurations needed for the three experiments. The viewing apparatus featured a removable central divider, and two versions of a front panel facing the participant: one with a single central viewing aperture, and one with two viewing apertures side by side. The EnChroma and control filters were embedded into frames to allow them to be affixed to any of the viewing apertures on either of the front panels, allowing single filter viewing or tandem filter viewing within one experimental session. Between tasks the participant was asked to step outside the experimental room, allowing the experimenter to alter the apparatus without the participant’s knowledge. As the
viewing apertures were backlit in otherwise dark conditions, participants were unable to
differentiate the EnChroma filter from the control filter.

Experiment 1 (colour matching task) required the stimulus space to be bisected, with
the target alone visible through filter A, and the matching array visible through filter B,
and then repeated with the filters reversed. To achieve this, a central wall was added,
and the participant-facing wall had two viewing apertures, to which the filters were
attached.

Experiment 2 (discrimination task) and Experiment 3 (rating task) required a single space
to present the stimuli, but for the task to be repeated with the experimental and control
filters separately. To achieve this no central divider was used, and a single aperture was
used on the side of the box facing the participant. The aperture containing the filter was
replaced in the participant’s absence. Experiment 3 (rating task) included a training phase
which required the participant to briefly point to stimuli. This required a curtained
window in the lower part of the participant-facing wall. The curtain across this space
stopped any light escaping during the experiments.

All sides of the apparatus were coated in Stuart Semple’s Black 2.0 paint (CultureHustle,
Dorset, UK) to minimize stray light. Stimuli were presented manually by a researcher on
the other side of the box, shielded from view by a black curtain, with only black-gloved
hands visible to the participant.
3.3.6 Procedure

Two sessions were held with each participant separated by 4-8 days, before and after a period of self-directed use of the filter where participants were loaned the filter and asked to use them for a minimum of 10 hours. Each session included three experiments: Experiment 1 (Colour Matching task), Experiment 2 (Discrimination task) and Experiment 3 (Rating task). Experiments were conducted in randomized order, and the entire session lasted approximately 90 minutes.

The colour matching experiment was carried out with the viewing apparatus segmented into two spaces with one side viewable through the EnChroma filter, and the other side viewable through the control filter. Filter conditions were swapped half-way through the Colour Matching experiment.
The Discrimination task and Rating Task were conducted without the divider, with the one filter aperture to view the entire stimulus space, and the experiment repeated for each filter condition.

3.4 Experiment 1: Colour Matching Task

3.4.1 Stimuli
23 surfaces were selected to be targets from the subset of Munsell surfaces of Value 5 (Glossy edition, Pantone, Michigan USA). The targets used in trials 1 to 12, where targets were viewed under the control filter, are plotted in Figure 5 (a), and the targets used in trials 13 to 23, where targets were viewed under the EnChroma filter, are plotted in Figure 5 (b). Munsell surfaces with the most similar chromaticities to each target when calculated in the opposing filter condition were identified as potential matches. EnChroma matches (red circles) to targets presented under the control filter (black crosses) are shown in Figure 5 (c), and control filter matches (black circles) for targets presented under the EnChroma filter (red crosses) are shown in Figure 5 (d). As participants were required to switch between the control and EnChroma filters repeatedly within a short space of time, the predictions were based on the modelled chromaticities which were not corrected to a common white point (which accounts for adaptation), since the side-by-side viewing of stimuli under both filter conditions allows minimal adaptation. The matching array included all non-neutral Value 5 Munsell surfaces (N=221), shown in Figure 6 (b).
Figure 5. (a, b) The targets used in the colour matching task, divided into trials 1-12 (a) presented under the control filter, and trials 13-23 (b) presented under the EnChroma filter. (c, d) The predicted matches to the targets, identified as the surface with the closest chromaticity in the opposing filter condition. Targets are indicated by “X”, and the closest matches under the opposing filter condition are indicated by the neighbouring circles (connected by blue semi-transparent shading). The chromaticities of all targets and predicted matching surfaces presented under EnChroma are plotted in red, and the chromaticities of all targets and predicted matching surfaces presented under the control filter are plotted in black. Trials 1 to 12 (a) involved targets presented under the control filter, and matches (c) selected from the array presented under the EnChroma filter. Trials 13-23 (b) involved targets presented under the EnChroma filter, and matches (d) selected from the array presented under the control filter.
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<tr>
<td>'CGG50004.DX'</td>
<td>3: 7.5 Green 5 4: 10 Green-yellow 5 4</td>
<td>5: 2: 7.5 Green-yellow 5 7</td>
<td>'CBB5001.DX'</td>
</tr>
<tr>
<td>'APB5004.DX'</td>
<td>4: 2.5 Purple-blue 5 4: 2.5 Blue-green 5 2</td>
<td>5: 2: 7.5 Green-yellow 5 7</td>
<td>'ABG5001.DX'</td>
</tr>
<tr>
<td>'ABG50101.DX'</td>
<td>5: 2.5 Blue-green 5 10: 7.5 Green 5 8</td>
<td>5: 2: 7.5 Green-yellow 5 7</td>
<td>'CGG5008.DX'</td>
</tr>
<tr>
<td>'CB5B9008.DX'</td>
<td>6: 7.5 Purple-blue 5 8: 5 Purple-blue 5 4</td>
<td>5: 2: 7.5 Green-yellow 5 7</td>
<td>'BFP5004.DX'</td>
</tr>
<tr>
<td>'BPF5004.DX'</td>
<td>7: 5 Purple 5 4: 5 Yellow-red 5 1</td>
<td>5: 2: 7.5 Green-yellow 5 7</td>
<td>'BYR5001.DX'</td>
</tr>
<tr>
<td>'ARR5002.DX'</td>
<td>8: 2.5 Red 5 2: 7.5 Yellow 5 2</td>
<td>5: 2: 7.5 Green-yellow 5 7</td>
<td>'CYY5002.DX'</td>
</tr>
<tr>
<td>'DF5B9008.DX'</td>
<td>9: 10 Red-purple 5 8: 2.5 Yellow-red 5 6</td>
<td>5: 2: 7.5 Green-yellow 5 7</td>
<td>'ARY5006.DX'</td>
</tr>
<tr>
<td>'DYY5004.DX'</td>
<td>10: 10 Yellow 5 6: 10 Yellow 5 6</td>
<td>5: 2: 7.5 Green-yellow 5 7</td>
<td>'DYY5004.DX'</td>
</tr>
<tr>
<td>'BRP5006.DX'</td>
<td>11: 5 Red-purple 5 6: 5 Yellow-red 5 4</td>
<td>5: 2: 7.5 Green-yellow 5 7</td>
<td>'BYR5004.DX'</td>
</tr>
<tr>
<td>'CYR5010.DX'</td>
<td>12: 7.5 Yellow-red 5 10: 2.5 Yellow 5 8</td>
<td>5: 2: 7.5 Green-yellow 5 7</td>
<td>'AYR5008.DX'</td>
</tr>
</tbody>
</table>

Table 1. The Munsell names of each of the targets and the identities of the predicted matches, including the chromas of predicted targets and match pairs. The difference in chroma between the target and predicted match denotes the predicted change in physical saturation attributable to the EnChroma filter.

3.4.2 Procedure

The colour matching task required participants to identify a match from an array presented in the opposing filter condition to the filter condition the target was viewed under. The two filter conditions, control and experimental, were unknown to participants, and the order of filter conditions and trials were randomized.

The target and matching array were presented in either side of a bisected box, with separate viewing apertures to each side (Figure 6, a). A single Munsell target was
presented in one half of the viewing apparatus. The participant was required to verbally identify a colour match using the coordinates written on an array of Munsell surfaces presented through the separate aperture. The matching array was split between two boards, and the participant was presented with both boards on each trial (Figure 6b). There were no time limits and participants were permitted to view target and array repeatedly. If no single surface was a perfect match, the closest match or a range of matches were requested. Four participants repeated the trials twice, completing 46 trials per session, before the procedure was shortened to reduce participant fatigue. The remaining 6 participants carried out 23 trials per session.

Figure 6 (a) A representation of the viewing apparatus, divided into two to create two spaces viewable under different filters. On the left the trial target is viewed under filter A, and the matching array viewed under filter B. Matches were identified verbally using a coordinate system. (b) The 2 panels of the matching array. (c) A schematic of a trial, where a more saturated match is expected when the target is viewed under the EnChroma filter. The arrow indicates surfaces that have the same Munsell chroma in the two filter conditions, but a more saturated match (black circle) is expected to be chosen among surfaces presented under the control filter, if the EnChroma filter increases perceived saturation.
3.4.3 Results

Figure 7. Target chromaticities and mean match chromaticities made by the 10 participants. (a) Targets viewed under the control filter, matches selected under EnChroma, pre-habituation. (b) Targets viewed under the EnChroma filter, matches selected under the control filter, pre-habituation. (d) Targets viewed under the control filter, matches selected under EnChroma, post-habituation. (e) Targets viewed under the EnChroma filter, matches selected under the control filter, post-habituation. (c) and (f) show mean matches with the habituation conditions combined. In all panels red data points indicate predictions or target chromaticities under EnChroma, and black data points indicate predictions or target chromaticities presented under the control filter. Crosses indicate target chromaticities, filled circles observed matches and open circles predicted matches.

The matches selected, shown in Figure 7, broadly follows the pattern predicted by the model, implying that EnChroma increases the perceived saturation of physical surfaces. When the target was presented under the control filter and the matching array under EnChroma (Figure 7a-c), the matches selected were systematically closer to the achromatic centre of the MacLeod Boynton (1979) chromaticity diagram than the targets, indicating that surfaces of lower saturation were matched to targets with greater physical
saturation. When the target was presented under EnChroma and the matching array under the control filter (Figures 7b-d) participants consistently selected surfaces with greater saturation as matches to lower saturation targets. Figure 8 presents the absolute change in L/(L’+L) alone between target and matched surfaces, collapsed across the two filter conditions as a proportion of the deuteranomalous L/(L’+L) gamut defined in Chapter 2, Section 2.2.3. When presented against the model predictions (blue bars) the observed matches frequently indicated a stronger change in L/(L’+L) than predicted by the model.

![Graph](image)

**Figure 8.** The difference in |L/(L’+L)| between the target chromaticity and the chromaticity of the mean match as a percentage of L/(L’+L) gamut, as described in Chapter 2. Trials are plotted in order of the value of L/(L’+L) of the control-filtered target, from teal to cherry. The changes in chromaticity predicted by the model are shown in blue, mean observed changes for the pre-habituation stage are shown in pink and for the
post-habituation stage in red. 95% confidence intervals are indicated by the error bars for both pre-habituation and post-habituation matches.

Table 2. Correlations between predicted and observed matches. a) Correlation between the chromaticity of observed matches and model predictions without \((L/L'+L)\) and with \((L/(L'+L)_w)\) white point correction. b) Correlation between predicted changes in \(|L/(L'+L)|\) as percentage of gamut, and the observed changes, also as percentages of the gamut. c) Correlations between the observed change in \(L/(L'+L)\) and, and the unfiltered \(L/(L'+L)\) values. d) Paired t-test between average changes (across hues) in \(|L/(L'+L)|\) conferred by the EnChroma filter compared to the control filter, between habituation conditions.

3.4.3.1 Correlation between matches and model predicted matches

A stronger correlation was found between the \(L/(L'+L)\) values of the observed matches, and the \(L/(L'+L)\) values of matches predicted by the model when there was no white-point correction applied, than when a white point correction was applied, for both habituation conditions (Table 2, a). This finding validates our choice to model the effect of EnChroma for this test without a white point correction.

3.4.3.2 Correlation between observed effects vs the predicted effects
A Spearman’s correlation revealed a moderate to strong positive relationship between the changes in \( \frac{L}{L'+L} \) predicted by the model, and the changes in \( \frac{L}{L'+L} \) observed in participants’ matches, both before habituation (Table 2, b).

3.4.3.3 Correlation between sizes of effect and the \( \frac{L}{L'+L} \) values of targets

In Chapter 2, we found correlations between the size of effect predicted from the EnChroma filter and the starting \( \frac{L}{L'+L} \) values of the modelled surfaces (Kendall’s tau \( r(46)=.877 \ p=<.0001 \)). We found a similar correlation between the mean \( \frac{L}{L'+L} \) values of the observed matches and unfiltered \( \frac{L}{L'+L} \) chromaticities of the targets both pre-habituation post-habituation (Table 2, c).

3.4.3.4 Effect of habituation

A paired t-test was conducted on the mean changes in \( |\frac{L}{L'+L}| \) conferred by the EnChroma filter relative to the control filter. No significant effect of habituation condition was found (Table 2, d).
3.5 Experiment 2: Discrimination task

3.5.1 Stimuli

Figure 9. (a) A representation of the viewing apparatus, with the 4AFC stimuli presented through one filter aperture. (b) Three stimuli from the red set, alongside a representation of the monotonic scales of stimuli. (c) Reflectance spectra of the 10th stimulus from each hue set. (d) The chromaticities of all stimuli when modelled under the control filter (black points) and when modelled under the EnChroma filter (red points). Chromaticities are expressed relative to the white point (the chromaticity of the distractor squares).

The stimuli for the discrimination task were surfaces hand-coated in an acrylic suspension of pigment (Figure 9, a), set into black frames, presenting three white squares and one colored target square in a 2x2 arrangement, to allow rapid manual randomization of the target surface’s location (by manual rotation) within the set of four (Figure 9, b, left). The saturation of the target surfaces within the stimulus set increased
monotonically for 18 steps from white in seven hue directions (Figure 9, b). An example reflectance spectrum from the 10th target for each of the hue directions is shown in Figure 9 (c). Figure 9 (d) shows the chromaticities (relative to the white point) of all target surfaces under the control filter (black circles) and under the EnChroma filter (red circles). The chromaticities of the surfaces under the EnChroma filter are further from the white point than the chromaticities of the surfaces under the control filter, indicating that EnChroma should enhance their perceived saturation.

Figure 10. (a) The modelled $|L/(L'+L)_w|$ chromaticities for each step in the set of stimuli along each colour axis under the control filter (coloured bars) and under the EnChroma filter (red points), indicating the enhancements in $L/(L'+L)$ by EnChroma predicted by the model. (b) Predicted reductions in threshold for each hue by the EnChroma filter given a hypothetical threshold of step 8 with the control filter.

The predicted effects of the EnChroma filter for each stimulus ($|L/(L'+L)_w|$) are plotted in Figure 10 (a). The figure shows that smaller enhancements in $L/(L'+L)$ are predicted for the yellow hue set than for the other hue sets. The more saturated the control filtered chromaticity, the greater the predicted enhancement in $L/(L'+L)$ (in agreement with findings of the model presented in Chapter 2, Section 2.3.2). If the model’s predictions are correct, the observer will receive the required chromatic signal for discrimination,
from a less saturated stimulus under the EnChroma filter than under the control filter. The resulting predicted reduction in discrimination threshold is represented in Figure 10 (b), where the lengths of the bars indicate the reduction in \( \frac{L}{(L'+L)} \) needed to meet threshold, if the control filtered threshold were at step 8. Step 8 was selected arbitrarily, to indicate potential reductions in threshold. The change in threshold was predicted as the difference between the \( \frac{L}{(L'+L)} \) value of control filtered 8th surface and that of the control filtered surface with a greater than or equal \( \frac{L}{(L'+L)} \) value when viewed under EnChroma. For example, the \( \frac{L}{(L'+L)} \) value of the 5th orange surface under EnChroma exceeds that 8th orange surface under the control filter. The predicted threshold is the difference between the \( \frac{L}{(L'+L')} \) values of the 5th and 8th surfaces, both under the control filter. Reductions in threshold are predicted to be greatest for the orange hue set, roughly equal for red, green, teal, and blue, smaller for purple, and minimal for yellow.

3.5.2 Procedure
In a four-alternative forced choice task, participants were asked to identify the colored surface on each trial. Stimuli were presented manually in a 1-up 1-down staircase procedure. Staircases began with the maximally saturated stimulus from each colour axis. Staircases were terminated after 5 reversals. One staircase was run for each of the 7 colour sets, and all 7 colour sets were completed under one filter condition before changing the filter. The order of colour sets and condition were randomized. Each participant completed the task four times, once under each filter condition at the pre-habituation timepoint and again at the post-habituation timepoint.
3.5.3 Results

Figure 11. Mean differences in threshold between the control filter and EnChroma filter conditions for the 10 participants are shown by the coloured bars. Hatched coloured bars indicate the mean from the pre-habituation session, and the solid bars indicate the mean from the post-habituation session. Predicted changes in threshold based on the control-filtered thresholds are indicated by wide blue bars. 95% Confidence intervals for both mean matches and model predictions are indicated by the error bars.

Table 4. T-test results from comparisons of thresholds between filter conditions for (a) each hue, and (b) comparing overall threshold changes between habituation conditions.

<table>
<thead>
<tr>
<th>Filter comparison per hue</th>
<th>Red</th>
<th>Orange</th>
<th>Yellow</th>
<th>Green</th>
<th>Teal</th>
<th>Blue</th>
<th>Purple</th>
</tr>
</thead>
<tbody>
<tr>
<td>p</td>
<td>0.000366</td>
<td>0.001866</td>
<td>0.934296</td>
<td>0.613343</td>
<td>0.030969</td>
<td>0.012214</td>
<td>0.167165</td>
</tr>
<tr>
<td>t</td>
<td>-4.324241</td>
<td>-3.609937</td>
<td>-0.083540</td>
<td>0.513759</td>
<td>-2.330224</td>
<td>-2.769251</td>
<td>1.436350</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>b) Habituation comparison</th>
<th>p</th>
<th>t</th>
</tr>
</thead>
<tbody>
<tr>
<td>Red</td>
<td>0.295800</td>
<td>-1.053472</td>
</tr>
</tbody>
</table>

For each staircase, discrimination threshold was calculated as the level of the 5 reversals. The changes in discrimination thresholds between the control filter and the EnChroma filter conditions are plotted in Figure 11. The only threshold that reduced with the EnChroma filter for all participants was that for red hues, which reduced by an average of -0.000484 ΔL/(L’+L) (Table 3). Paired t-tests were carried out for each hue, and once
adjusted for multiple comparisons using a Bonferroni correction, the only thresholds significantly different between filter conditions were for red; \( t(19)=4.324, p<.001 \), and orange; \( t(19)=-3.609, p=.0018 \). Thresholds for red significantly reduced, whereas the thresholds of all other colours either increased or were not significantly different between filter conditions (Table 4a). New predicted thresholds were generated as described in Section 3.5.1 but using the observed mean thresholds under the control filter condition to predict mean thresholds under the EnChroma filter condition. These are indicated in Figure 11 by the light blue shaded bars. The results support a partial effect of EnChroma at reducing discrimination thresholds, since an effect was found only for the hue that was predicted to have the greatest reduction.

A t-test comparing the effect of the habituation period on the threshold difference between filter conditions found no effect (\( t(69)=-1.0534, p=.296 \)).

3.6 Experiment 3: Rating task

The rating task aims to identify, via changes to ratings of dissimilarity, represented geometrically using multidimensional scaling, whether increases in chromatic signals by the EnChroma filter result in increases in perceived saturation.

3.6.1 Stimuli

Thirteen Munsell surfaces of high chroma (N=9) and low chroma (N=4) chroma were selected for their approximate equidistance in the MacLeod Boynton chromaticity diagram, and because, under halogen illumination, EnChroma is predicted to increase
L/(L’+L) saturation more than S/(L’+L) saturation (Figure 12 c). We expected that the changes in chromaticity predicted by the model would result in corresponding changes to ratings of dissimilarity. We also expected that the asymmetry of the predicted changes in chromaticity between the two colour channels would be preserved in the ratings of dissimilarity. This difference changes to dissimilarity ratings between the two colour channels then should be visible in the relative spacings of the stimuli along the two corresponding axes in MDS solutions recreated from the dissimilarity ratings.

As well as the change in dispersion along the two colour axes by EnChroma predicted by the model, the model also predicted that some of the Munsell surfaces would show a larger change in chromaticity than others. We therefore divided the stimuli into two sets: Six surfaces were assigned to the low prediction group (surfaces 1, 4, 8, 11, 12 and 13; Figure 12 c) because their predicted changes in chromaticity under EnChroma were low, and seven surfaces were assigned to the high prediction group (surfaces 2, 3, 5, 6, 7, 9 and 10; Figure 12 c) because their predicted changes in chromaticity under EnChroma were high.
Figure 12. (a) A diagram of the apparatus, indicating single filter used within each filter condition. Stimuli were presented pairwise until pair within the set of 13 stimuli had been presented. (b) A photograph of the stimuli taken during the training phase where all stimuli were presented to give the participant a chance to calibrate their ratings. To reinforce this ‘calibration’, participants were asked to indicate the pairs they would give a minimum dissimilarity rating, a maximum dissimilarity rating and a medium dissimilarity rating. (c) The chromaticities of the 13 stimuli modelled under the control filter (x marks), and under the EnChroma filter (circle marks), under halogen illuminant.

3.6.2 Procedure
The 13 Munsell surfaces were presented pairwise to be rated for dissimilarity. Participants were instructed to rate identical appearance as 0 and the most different as 9. The set of pairs included 4 duplicates to establish a baseline of surfaces rated against themselves. Two ratings were collected for each pair making 160 ratings in total.

Before testing began for each filter condition a short training session established the range of chromatic differences by presenting all chips simultaneously (Figure 12 b), with the participant was asked to identify pairs they would give dissimilarity ratings of 0, 9 and 5. This was intended to improve the quality of the ratings given within the session
as it allowed the participant to calibrate their ratings against the range of colour differences available within the set.

During testing only two surfaces were viewed at any given time, presented manually by an experimenter wearing black sleeves and black gloves, and otherwise hidden from view. The participant was asked to give a verbal rating for how dissimilar the surfaces looked, from 0 to 9.

The stimuli were viewed through a signal aperture, with experimental and control filters used in separate repetitions of the task (Figure 12, a), conducted in randomized order.

3.6.3 Data processing
Data processing was done using custom code written in Matlab (MathWorks Inc., Massachusetts, USA). Trial duplicates were averaged before the tied rank of the rating for each pair was found. Non-metric multidimensional scaling was performed on the resulting ranked dissimilarity matrix, specifying 2D MDS solutions, which represent the set of perceived dissimilarities as 2D Euclidean distances.

To relate the distances between stimuli in the MDS solution to the predictions made in MacLeod Boynton chromaticity diagram, Procrustes analysis was used to optimally align the dimensions of the MDS solution with the cardinal axes of the deuteranomalous variant of the MacLeod Boynton chromaticity diagram, $L/(L'+L)$ and $S/(L'+L)$. We allowed reflection and rotation in the Procrustes analysis, but not scaling, so the relative positions of the stimuli within the MDS solution remained unchanged, as do the relative distances between stimuli along orthogonal axes. Procrustes-transformed coordinates of
the stimuli in the MDS-solution were averaged across participants to give group average results.

3.6.3 Results

Figure 13. Group average MDS solutions plotting the positions of the surfaces viewed under the control filter (hollow circles) and viewed under the EnChroma filter (filled circles). (a) The group average MDS solution for ratings given pre-habituation; (b) The group average MDS solution for ratings given post-habituation. Dimension 1 is aligned with the L/(L'+L) axis of the MacLeod Boynton Chromaticity diagram, and Dimension 2 is optimally aligned with the S/(L'+L) axis via Procrustes transformation allowing rotation and reflection only.

The average MDS solutions across participants are shown in Figure 13. The solutions are given credibility by their arrangement forming a colour wheel, with the desaturated surfaces close together near the centre of the solution, replicating previous studies of colour representation using MDS (e.g., Boehm et al. 2014; Paramei & Cavonius, 1999). In the pre-habituation condition, the perceived differences between surfaces viewed with the EnChroma filter are elongated along dimension 1 compared to the perceived
distances between the same surfaces viewed with the control filter. The majority of the surfaces with high saturation show increased perceived saturation of $L/(L'+L)$ under the EnChroma filter than under the control filter, in that the surfaces under EnChroma are positioned in the MDS solution further away from the achromatic centre than the surfaces under the control filter. There is no consistent effect evident in the post-habituation condition.

Figure 14. Mean differences between the absolute positions of each surface in the EnChroma filter condition and the absolute positions of each surface in the control filter condition. Positive values indicate an enhancement to perceived saturation along the $L/(L'+L)$ axis by EnChroma. (a) Mean differences in the pre-habituation condition; (b) Mean differences in the post-habituation condition. Error bars are 95% confidence intervals.
Figure 14 shows the differences between the absolute values along the first dimension of the MDS solution (which has been aligned with $L/(L'+L)$ by Procrustes transformation). Thus, positive differences occur when the surface is further from the achromatic centre of the MDS solution under the EnChroma filter than under the control filter and negative values occur in the converse situation. Any positive values imply an enhancement to perceived saturation (moving the surface away from the achromatic centre) in the EnChroma filter condition relative to the control filter condition. The figure shows that in the pre-habituation condition show positive differences, consistent with an enhancement to perceived saturation by the EnChroma filter.

![Table 5](image)

Table 5. (a) Results of a one-sample t-test on the differences plotted in Figure 14 for surfaces 2, 3, 5, 6, 7, 9 and 10 for the pre-habituation condition (Pre-H) and the post-habituation condition (Post-H). (b) Results of a paired t-test on the differences between the high and low predicted change stimuli, for the pre-habituation condition (Pre-H.) and post-habituation condition (Post-H.). (c, d) Results of ANOVAs testing the $L/(L'+L)$ distance in the direction of the predicted effect for the pre-habituation condition (c) and post-habituation condition (d).

We conducted a one-sample t-test on 7 of the differences, which were predicted to be substantial by our model (samples 2, 3, 5, 6, 7, 9 and 10; see Figure 12). The t-test showed that the differences are significantly greater than 0 in the pre-habituation
condition (Table 5a, Pre-H), implying an effect of the EnChroma filter in enhancing perceived saturation along the L/(L’+L) axis. For the post habituation condition, the differences between the absolute values along the first dimension of the MDS solution show no consistent pattern and are not significantly different from 0 (Table 5a, Post-H).

To investigate any differences in the changes in position of surfaces in the MDS solutions between the EnChroma filter and the control filter that may be specific to particular colours, a one-way ANOVA was conducted on the mean differences plotted in Figure 14. The ANOVA found no significant effect of colour either for pre-habituation or post-habituation (Table 5c and d). Similarly, we conducted a paired t-test on the mean differences for the low prediction group and the high prediction group (see Section 3.6.1) and no significant difference was found, either for pre-habituation or post-habituation.

3.7 Discussion
3.7.1 Colour matching task
The findings of the Colour Matching task followed the predictions of the model both in the predicted shifts in chromaticity and in the predicted increases in saturation caused by the EnChroma filter. The broad agreement between model predictions and the observed colour matches provides validation for the model. In some cases, the size of the predicted enhancements in saturation by the EnChroma filter exceeded those predicted by the model, but the model was based on an ‘average’ anomalous observer and the size of the predicted colour changes are observer-dependent.
This experiment is one of the first positive findings for the effectiveness of the EnChroma filters on the colour perception of anomalous trichromats for stimuli that are not part of CVD screening tests. Gómez-Robledo et al., (2018) conducted a colour naming experiment on the effect of EnChroma filters which did not identify any systematic changes in colour naming. It is possible that there was some change in perception of their stimuli attributable to the EnChroma filters but that it was too subtle to be detected in changes in naming, which involve categories of hues.

The sizes of the enhancements in saturation of colours by EnChroma were the same between the pre-habituation and post-habituation conditions. Werner et al., (2020) identified a long-term effect of the filters, observing an increased chromatic contrast response measured without the filters after prolonged filter use. This finding suggests that experience with the EnChroma filters can trigger a long term gain in colour contrast, perhaps via perceptual learning. We did not observe any increase in colour enhancements between post-habituation and pre-habituation conditions, which is inconsistent with the evidence of perceptual learning identified by Werner et al., (2020).

3.7.2 Discrimination task
Results from the discrimination task indicated a significant reduction in threshold by the EnChroma filter for only one hue, red. Discrimination thresholds for the other 6 hues tested did not differ significantly between filter conditions. Our results provide only partial support for the model’s prediction, as the red hue was predicted to receive the greatest reduction in discrimination threshold, when taking into account the observed group average thresholds with the control filter (Figure 11).
It is possible that our choice of control filter has contributed to our mainly negative findings for the effect on colour discrimination thresholds of the EnChroma filter. For overall broad spectrum attenuation, the 41.35% transmission of the control filter matched the 40.64% transmission of the EnChroma filter closely. However, when for the proportion of that light detectable by the L and L’ cones, the difference between the attenuations of the two filters is greater: the control filter has a transmission of 33.3%, whereas the EnChroma filter has a transmission of 20.7%. Because colour discrimination thresholds increase as luminance reduces (e.g. Pridmore & Melgosa, 2005), this substantial reduction in radiance in the spectral region we tested could have resulted in threshold elevations for the EnChroma filter relative to the control filter, counteracting the potential effect of the notch filter in reducing colour contrast discrimination thresholds.

3.7.3 Dissimilarity task
The results of the dissimilarity task provided only borderline support for an effect of the EnChroma filter. In the pre-habituation condition the EnChroma filter caused the positions of surfaces in the MDS-reconstructed colour space to be significantly further from the achromatic centre of the solution than with the control filter, along the axis aligned with \( L/(L'+L) \). However, the effect size was small \( t(9) = 2.59, p = 0.03 \), and no significant effect was observed in the post-habituation condition.
It is possible that that design of the dissimilarity experiment hindered its ability to detect enhancements in colour contrast by the EnChroma filter. We selected the halogen illuminant for its low radiance at short wavelengths to constrict the predicted changes in
chromaticity along the \( S/(L'+L) \) dimension of deuteranomalous colour vision. However, the salience of colour changes are more likely to be relative to the starting chromaticities rather than the absolute sizes of the colour changes. EnChroma may be expected to produce a similar percentage change in chromaticity along both the \( L/(L'+L) \) and the \( S/(L'+L) \) axes, thus reducing any observable effect in an MDS solution where ratings are relative to the maximum available within the whole stimulus set.

3.7.4 Impact of habituation
All three experiments were repeated at a second timepoint after participants had used the EnChroma filters for a minimum of 10 hours in photopic conditions. The changes in chromaticity conferred by EnChroma in colour matches observed in Experiment 1 did not significantly differ between habituation conditions. In the results of Experiment 2 there was no evidence of the EnChroma filter impacting discrimination thresholds differently between habituation conditions (Table 4, d), and in both habituation conditions the only significant effect of the EnChroma filter was on the red stimuli. However, in the results of Experiment 3 we observed a significant effect of the EnChroma filter on enhancing \( L/(L'+L) \) colour differences in the pre-habituation condition but not in the post habituation condition, providing tentative evidence that any effect of the filters on the representational space of colours may be short-lived.
3.8 Conclusions and future directions

Our findings constitute some of the first strong evidence supporting claims by EnChroma Inc. that their filters can have a beneficial effect on perceived saturation for anomalous trichromats. Our results validate the predictions of the model presented in Chapter 2. Although findings from Experiment 1 show that even surfaces with initially low saturation are predicted to receive an enhancement in saturation from the EnChroma filter, in Experiment 2 the EnChroma filter was found to have an effect only for red in reducing discrimination thresholds. Results from Experiment 3 imply that any expansion in the representation of colours along the L/(L'+L) axis may be short-lived and disappear with adaptation after the filter has been worn habitually for about 10 hours. Future work is needed to investigate whether changes in discrimination threshold by the EnChroma filter could be better measured by matching the luminance attenuation between the filter conditions in the medium and long wavelength spectral range, since this may better isolate the effect of increased chromatic contrast. The procedure used in Experiment 3, the rating task, could be improved by alternating the filter used within each session, so that participants are not given a chance to recalibrate their scale of ratings between the filter conditions. This may allow an effect to be detected that could have been lost in the procedure as carried out in this study. Further work could extend understanding of the effect of the EnChroma filters by conducting similar research with protanomals, who are predicted to receive a slightly different effect from the filters (see Chapter 2).
4.0 Abstract
The Ishihara Plates test is one of the most established and widely used means of identifying colour vision deficiencies. However, its use in screening (for participants who took part in the study described in Chapter 3) returned a higher proportion of dichromats among colour deficient observers than prevalence studies predict. Some of the literature examining the effectiveness of the Ishihara Plates test has identified weaknesses when screening for milder anomalous trichromacy, and investigations of the lighting environment used for testing are either limited or out-dated. We present an investigation into possible causes of this under-representation of mild anomalous trichromacy in people screened for CVD using the Ishihara plates test using a joint modelling and behavioural approach. The chromatic signals expected to contribute to false negative readings by anomalous trichromats were predicted by measuring the difference in chromaticity between the ground and pseudoisochromatic portions of the plate. Predicted signals from 5 plates were compared for 7 editions of the Ishihara plates test, for six observers with three severities of anomalous trichromacy, under 7 illuminants. The impact of edition was tested behaviourally with 35 CVD observers, which corroborated the minimal effect of edition predicted by the model. A significant negative relationship was found between predicted colour signals for anomalous trichromats and false negative plate readings (τ =-0.4159, p<.0001) suggesting that residual observer-specific colour signals in portions of plates designed to be isochromatic may be
contributing to false negative readings. Our findings suggest that illuminant has a larger bearing on the colour signals available for the protanomalous observer than the deuteranomalous observer, and plate having a greater effect on deuteranomalous chromatic signal than protanomalous.

4.1 Introduction

4.1.1 Red-green colour vision deficiency
Colour vision is based on a comparison of signals from three classes of cone in the retina, sensitive to long- (L), medium- (M) and short- (S) wavelengths of light. Colour vision deficiencies (CVDs) arise from genetic mutations which result in the presence of an anomalous cone class or in one cone class being missing from the retina entirely (Bosten, 2019). A missing cone class results in dichromacy, a severe colour vision deficiency in which colour vision signals are constructed from the remaining 2 cones classes only. Deuteranopia is caused by a missing M cone class and deuteranopic colour vision is based on a comparison of signals sent by the remaining L and S cone classes (Sharpe et al., 1999). Protanopia results from a missing L cone class, meaning colour vision is based on a comparison of M and S cone signals. The absence of an entire cone class results in two-dimensional rather than three-dimensional colour vision: there is a dimension of trichromatic colour vision that is unavailable to dichromatic observers. It is possible to represent this dimension of imperceptible colour differences as “confusion lines”, drawn through colour space (Fry, 1992). The Ishihara Plates test uses chromaticities that fall along these confusion lines as means to diagnose colour vision deficiency (Dain, 1998).
Anomalous trichromacy is a milder form of CVD where three cone classes are present but two of the cone types are more similar in their spectral sensitivities than in normal trichromacy (Bosten, 2019). The two common forms of anomalous trichromacy are deuteranomaly, when an anomalous L’ cone class is present in addition to the normal L and S cone classes, and protanomaly in which an anomalous M’ cone class is present alongside the normal M and S cone classes (Sharpe et al., 1999). The increased similarity between the sensitivities of two of the cone classes sensitive in the medium and long-wave parts of the spectrum results in a restriction in the range of available cone-opponent signals, and in weaker colour percepts along this axis (Mollon, 1989). The weakened dimension of colour vision in anomalous trichromacy falls roughly (but not exactly) along the confusion lines for dichromats, but in anomalous trichromacy the available colour signals are weaker rather than entirely absent (Regan et al., 1993).

Due to polymorphisms in the genes encoding the L’ and M’ opsins, different individual anomalous trichromats have cone classes with different spectral sensitivities (Deeb, 2006). The severity of anomalous trichromacy is thought to be related to the degree of separation between the wavelength of greatest sensitivity of the anomalous cone and that of its closest neighbour, which can vary between 1 nm to 12 nm in different individuals, compared to ~30 nm for normal trichromats (Bosten, 2019). The smaller the spectral separation of peak sensitivities, the greater the reduction is thought to be in sensitivity to colour differences that rely on signals sent by the long and medium wavelength sensitive cone classes (DeMarco et al., 1992). The spectral separation is referred to as the $\Delta \lambda_{\text{max}}$, the difference between $(\Delta \lambda)$ the wavelengths ($\lambda$) of peak sensitivity ($\lambda_{\text{max}}$).
The gold standard in the classification of colour vision deficiencies is the Anomaloscope, which employs an adjustment task to measure Rayleigh matches, classifying observers according to the amounts of red and green light needed for a perceptual match to a spectrally pure yellow (Pokorny et al., 1982). Dichromats accept any mixture as a match. Compared to the mixture accepted by normal trichromats, deuteranomals require a greater proportion of green, and protanomals a greater proportion of red. Extreme anomalous trichromats are characterised by accepting a broader range of mixtures as a match, accepting normal trichromatic mixtures as well as mixtures typical of anomalous trichromats.

4.1.2 The Ishihara Plates test
The Ishihara Plates test is a physical book of plates, each comprising a figure-ground segregation task using chromaticities which fall along dichromatic confusion lines, selected to be indiscernible to dichromats or of reduced discriminability to anomalous trichromats. First published in 1906 (Dain, 2004) the test has been republished in many editions and is the most widely used tool for screening for CVD in the world (Birch, 2012). It offers high sensitivity and specificity (Krauskopf, 1998) with sensitivities (and specificities) of 98.7% (94.1%), 94.0% (95.4%), and 80.5% (100%) for fail criteria of 3, 6 and 8 errors respectively (Birch, 1997b). It also offers the benefits of being portable, unpowered and requiring minimal training to deploy. It is considered by some to be the gold standard for CVD screening (Krauskopf, 1998) and is commonly considered second only to the anomaloscope. The anomaloscope requires stable conditions and an electricity supply, which is not always practical in screening settings, is expensive, and is rarely
available outside Europe (Birch, 2012) and teaching institutions (Dain, 2004) contributing to the Ishihara plates test being the primary screening test used for CVD across the globe.

4.1.3 Task
The Ishihara plates test consists of a series of figure-ground segregation tasks, one per plate. The full test has 38 plates, and abbreviated versions have 24. In all instances the figure is either a serifered numeral or a pathway, provided as a non-lettered version of the task. The figure-ground segregation depends on sensitivity to chromatic information. Any available luminance signals for figure and ground segregation are masked by luminance noise provided as luminance variation among constituent dots. Although the figure is always centrally located, the spatial form of the numeral is masked by both the figure and ground being formed of tightly packed and evenly spaced discs of six sizes, distributed equally between the figure and the ground. The figure in each plate is formed of discs of three discrete chromaticities not found in the ground, and the ground consists of discs of three discrete chromaticities not found in the figure (see Figure 2 for an example plate). Identifying the target number requires successfully grouping the three figure chromaticities as separate from three ground chromaticities, as indicated descriptions of the task by people with CVD (Miyahara, 2009).

4.1.4 Plate Designs
The 38 Plate Edition includes 6 categories of plate: demonstration, transformation, vanishing, hidden digit, classification, and non-verbal. The demonstration plate is non-
diagnostic training plate indicating the task in the remaining plates by presenting an example numeral or pathway which is easily identifiable to all observers. Transformation plates provide positive diagnostic information by including two numerals, one visible to the normal trichromat but not the CVD observer and a second digit overlayered, which is visible to the CVD observer but less salient (in comparison to the first digit) for the normal trichromat. In vanishing plates there are digits visible to normal trichromats but not to observers with CVD. The hidden-digit design reverses the principal of the vanishing design, presenting a digit identifiable to CVD observers due to a luminance difference between figure and ground, which is masked for the normal trichromat by chromatic noise. Classification plates contain two digits, in which one digit is designed to be resolvable for a deutanope but unresolvable for a protanope and the other digit the reverse (Ishihara, 2014). The figure in the non-verbal design is a pathway across the plate rather than a numeral, designed for screening non-verbal or pre-literate people (Ishihara, 2014).

Those with milder anomalous trichromacy have greater chromatic signals available to them than those with more severe anomalous trichromacy or dichromacy. Some figures may therefore be discriminable to mild anomalous trichromats, leading them to give a reading expected from normal trichromats. For the classification plates, observers with mild anomalous trichromacy are expected to be able to identify both the deutan and protan digits (Ishihara, 2014), whereas dichromats are expected to identify only the digit targeted at their observer type. Due to variation in signals available to those with different levels of anomalous trichromacy, it is advised to have a criterion of at least 3 plate errors
before classifying an observer as CVD (Birch, 1997b). However, normal trichromats have been found to make up to 6 errors (Birch & McKeever, 1993).

4.1.5 Previous studies of the Plates test
4.1.5.1 Comparative studies

A great many investigations into the effectiveness of the Ishihara plates test have compared results to those from other forms of screening, in some cases finding flaws in the Ishihara Plates test, but in many cases finding the Ishihara Plates test superior to other tests of equal portability and accessibility (Belcher et al., 1958; Birch, 1997a, 2010; Birch & McKeever, 1993; Cosstick et al., 2005; Katavisto, 1961; Rodriguez-Carmona et al., 2012; Sloan, 1956). Studies comparing pseudoisochromatic tests have found the Ishihara plates test to be a superior screening tool to the HRR, Richmond HRR test (Birch, 2010), and the Ohkuma test (Birch & McKeever, 1993). An early spectrophotometric and colorimetric analysis (Lakowski, 1966) found the Ishihara Plates test to be similar to the HRR test in the contrasts between figure and ground chromaticities. The chromaticities used in the Dvorine test (1953) appeared to be similar to the Ishihara and HRR, but with the figure and ground chromaticities reversed. Assessment of diagnostic plates from the Ishihara, Dvorine, HRR and Tokyo tests (Umazume et al., 1954) revealed that the Ishihara plate was constructed very similarly to the Dvorine test (Lakowski, 1966).
4.1.5.2 Variation between plates

Although the Ishihara Plates test has a high sensitivity overall, variation in the effectiveness of different plate types has been identified (Belcher et al., 1958; Birch & McKeever, 1993; Rodriguez-Carmona et al., 2012; Sloan, 1956). Screening efficiency values calculated by combining the numbers of misreadings by normal trichromats and false negatives by observers with CVD have identified the most efficient plates as Transformation plates 2, 3, 6 and 8, and Vanishing plates 10, 11, 14 and 15 (Birch & McKeever, 1993). Hidden digit plates have been found to be ineffective for screening purposes, with a mean sensitivity of only 37.5% for the 9th and 1989 editions (Birch & McKeever, 1993), potentially due to usable signals from S cones for normal trichromats (Miyahara, 2009). When diagnosis is based on a subset of the Ishihara plates test rather than the full test, false negative readings for anomalous trichromats are more common. False negative readings have been found to be made by deuteranomalous observers over 50% of the time with three transformation plates and three hidden digit plates, while protanomalous observers have been found to make false negative readings of over 40% for only one hidden digit plate (Rodriguez-Carmona et al., 2012).

4.1.5.3 Variation between editions

The full Ishihara plates test has 38 plates, the abbreviated editions have 24 plates, and the concise edition has 14 plates. The plates included in the full test have followed the same spatial design since 1906, though the chromaticities have been noted to vary visibly between editions (Lee & Honson, 2003) and variation in diagnostic outcomes of different
editions has been found (Birch & McKeever, 1993). Colorimetric analysis has revealed that points in the diagnostic plates deviate from confusion axes by up to 5.5 degrees in CIE(x,y) space (Lee & Honson, 2003). The 1993 and 1997 editions have been found to be the most problematic from the small sample of editions studied by Lee and Honson (2003), who have advised colorimetric analysis of Ishihara editions before using them to diagnose anomalous trichromats.

4.1.5.4 Observer variation

The Ishihara Plates test has been found to have weaknesses in identification of milder cases of CVD (Birch & McKeever, 1993), with certain plates such as hidden plates found to be particularly ineffective (Belcher et al., 1958; Haskett & Hovis, 1987; Rodriguez-Carmona et al., 2012).

The recommended mechanism for identifying milder CVD with the Ishihara plates test is to adjust the fail criterion (Birch, 2010). This advice trades the specificity of the test against its sensitivity, enabling the tester to prioritise the avoidance of false positives or false negatives as the situation requires. Diagnostic advice provided with early editions of the Plates test recommended a pass criterion of three errors and a fail criterion of 6 errors to indicate CVD, leaving considerable room for unclassified cases. These criteria will hinder the test's effectiveness when screening for mild anomalous trichromacy. Lower fail criteria are often employed in research on anomalous trichromats, 6.8% of whom have been found to make fewer than 6 errors (Birch, 1997b). Normal trichromats
have been found to make up to 6 errors (Birch, 1997b), meaning the Ishihara plates test is unable to differentiate some mild anomalous trichromats from normal trichromats.

4.1.5.5 Variation in illumination

The recommended illuminant for testing colour vision is CIE Standard Illuminant C, a hypothetical illuminant resembling slightly blue daylight (Pokorny et al., 1982), which gives researchers the task of interpreting this ideal in the context of what is possible and practical in the testing environment. The impact of the spectral power distribution of the illuminant on the effectiveness of pseudoisochromatic plates has been investigated quite extensively, but many existing studies have focussed on outdated illuminants, either tungsten bulbs or specially designed bulbs that are no longer available (Hardy et al., 1946; Higgins et al., 1978; Johnson, 1992; Schmidt, 1952). Tungsten bulbs have since become the target of the European Union Directive (EC 244/2009) progressively banning less energy efficient modes of lighting, beginning with incandescent bulbs in 2009. Some research has acknowledged the difficulty of maintaining standards with changes in commercially available illuminants (Dain et al., 2020), and differences between products of the same category (Dain, 1998). Recent studies of the impact of LED illuminants have noted that spectral power at longer wavelengths reduces the number of errors made by observers with deutan deficiencies. Tamura et al., (Tamura et al., 2017) tested five deuteranopes and two deuteranomals on the Ishihara Plates test under LED illuminants peaking at 7 spectral positions ranging from 450 to 660 nm. Illuminants peaking at 590, 605, 630 and 660 nm were associated with reduced numbers of errors. The strongest effects were found for illuminants with peak spectral power at the longest wavelengths
tested, 660 nm, resulting in a 25% reduction in deutan errors. This finding indicates that illumination can have an impact on the effectiveness of the Ishihara Plates test as a screening tool for CVD. Due to the variety in spectra of LED illuminants, some recommendations focus on the CIE correlated colour temperature rather than the spectrum itself, advising a CCT of approximately 6500K for colour vision testing purposes (Dain et al., 2020; Pokorny et al., 1982). This approach may be problematic as there are a variety of spectra associated with each correlated colour temperature and thus the potential for observer metamerism with some Illuminants.

4.1.6 Rationale

Though many aspects of the Ishihara Plates test have been investigated, and there is a rich literature validating their use, assessments generally focus on one variable at a time. Previous research has highlighted substantial variation in the effectiveness of screening between plates and plate types, but this research did not investigate whether these differences are consistent across the many editions that have been printed. Similarly, colorimetric research has identified differences between editions, but has not identified the impact of this on screening effectiveness. Investigations assessing the impact of illumination have not previously been put in the context of the chromatic variation between plates and editions, and the interactions between these three variables have not been assessed. A comprehensive investigation that will assess the impact of these three variables together may offer insights into the amount of chromatic information contributing to false negative readings and may assist in future screening for mild anomalous trichromacy.
To predict the impact of different factors on the ability of the Ishihara Plates test to identify cases of mild anomalous trichromacy we created a model of the cone-opponent signals predicted to be available to such observers. Predicted signals were then compared between categories of plate, between different ages of edition, for different severities of anomalous trichromacy, and between different illuminants.

4.2 Modelling Investigation: Methods

4.2.1 Model

Figure 1. The physiologically accurate model of colour vision. The SPD of the illuminant (1) is multiplied by the reflectance spectrum of each sample from the Ishihara Plates test (2), representing the proportion of the light reflected at each wavelength which reaches the eye (3). The subsequent cone response as a function of wavelength (4) is the product of the spectral power distribution of light reaching the eye and the sensitivity of each cone class at each wavelength (3). The total response of each cone is calculated by summing wavelength-specific cone responses over all wavelengths (5). Lastly, the total responses of the cone classes are used to model the signals available in two post-receptoral colour channels (the axes of an observer-specific version of the MacLeod-Boynton (1979) chromaticity diagram), here represented for deuteranomalous observer, where \( L/(L'+L) \) replaces the normal trichromatic \( L/(L+M) \), and \( S/(L'+L) \) replaces the normal trichromatic \( S/(L+M) \).
Equation 1. The derivation of the respective activities of the L, M and S cone classes in response to a defined illuminant and surface reflectance, per wavelength.

\[ L = \int_{380}^{780} l(\lambda) R(\lambda) I(\lambda) \, d\lambda \]
\[ M = \int_{380}^{780} m(\lambda) R(\lambda) I(\lambda) \, d\lambda \]
\[ S = \int_{380}^{780} s(\lambda) R(\lambda) I(\lambda) \, d\lambda \]

A model of anomalous colour vision, similar to one previously published (Jordan et al., 2010), was used to estimate the signals available in the two cone-opponent colour channels in response to the spectra present in the plates. Equation 1 below describes how this model takes the product of the spectral power of the illuminant (Equation: I; Figure 1: step 1), the surface’s reflectance spectrum (Equation: R; Figure 1: step 2) and cone sensitivity functions constructed for a particular type of observer (Equation: l, m and s; Figure: step 3). The results are summed over all wavelengths (Figure 1 step 4) to calculate the resulting cone activities in response to the surface (equation: L, M and S; Figure 1: step 5). Summed cone activations used to calculate chromaticity coordinates for the MacLeod-Boynton chromaticity diagram (MacLeod & Boynton, 1979): \( L/(L+M) \) and \( S/(L+M) \), which provide estimates of the activities of two post-receptoral cone-opponent colour channels. Using this method, observer-specific chromaticity coordinates were constructed for anomalous trichromats by substituting the cone activities predicted for normal trichromats with those predicted for anomalous trichromats. The \( L/(L+M) \) channel (horizontal axis) is \( L(L'+L) \) in a deuteranomalous variant of the chromaticity
diagram, and $M'/(M+M')$ in a protanomalous variant. The normal trichromatic $S/(L+M)$ axis is $S/(L'+L)$ in the deuteranomalous variant and $S/(M+M')$ in the protanomalous variant.

4.2.2 Surfaces

The surfaces used in the model are the individual discs (each of uniform colour) from the Ishihara plates. The spectra of the surfaces were measured from the same locations from each of 5 plates in 7 editions of the Ishihara plates test. The seven editions used in the investigation are identified by their year of printing: 1963, 1975, 1981, 1991, 2010, 2013, and 2017. All editions used were 38 Plate editions, apart from 1963 which was a 24 Plate edition, which contains identical plates to those sampled from the other editions, though presented in a different order.

For each plate, 6 points were measured, including 3 from the background and 3 from the pseudoisochromatic figure (i.e., the figure designed to be indistinguishable to the observer it is designed to identify). In the case of transformation plates, figure points were taken from the part of the figure expected to be pseudoisochromatic for observers with CVD. In the case of the diagnostic plate, 9 points were measured; 3 from the background, 3 from the points designed to be pseudoisochromatic for deutans, and 3 from the points designed to be pseudoisochromatic for protans. Since each figure or background is made up of 3 discrete hues, all the relevant spectra with which the observer is expected to make the discrimination were sampled. An example plate showing the points sampled is shown in Figure 2.
Figure 2. Representations of a single transformation plate, highlighting the target designed to be visible for the CVD observer (top left) and the target designed to be visible to the normal trichromatic observer (bottom left). Centre: the locations of the chromaticities used in the model; three figure points (taken from the normal trichromat’s target), and three ground points.

<table>
<thead>
<tr>
<th>Sample #</th>
<th>Numeral shown</th>
<th>Plate number*</th>
<th>Plate type</th>
<th>Abbreviation</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>45</td>
<td>13 (8)</td>
<td>Vanishing</td>
<td>Va.1</td>
</tr>
<tr>
<td>2</td>
<td>7</td>
<td>15 (10)</td>
<td>Vanishing</td>
<td>Va.2</td>
</tr>
<tr>
<td>3</td>
<td>29</td>
<td>4 (2)</td>
<td>Transformation</td>
<td>Tr.1</td>
</tr>
<tr>
<td>4</td>
<td>3</td>
<td>7 (4)</td>
<td>Transformation</td>
<td>Tr.2</td>
</tr>
<tr>
<td>5</td>
<td>26</td>
<td>22 (15)</td>
<td>Diagnostic (Protan)</td>
<td>Di.1</td>
</tr>
<tr>
<td>6</td>
<td>26</td>
<td>22 (15)</td>
<td>Diagnostic (Deutan)</td>
<td>Di.2</td>
</tr>
</tbody>
</table>

* Plate numbers outside brackets refer to the location within 38 plate editions, the value in brackets indicates the position in 24 plate editions.

Table 1. Details of each sample used in the model. Plate number refers to the location within the 38-plate edition (bracketed number indicates the position within the 1963 24-plate edition).

The 5 plates modelled include two vanishing plates (Va.1 and Va.2; Plates numbered 13 and 15 in all editions apart from 1963 in which they are Plates 8 and 10), two transformation plates (Tr.1 and Tr. 2; Plates numbered 4 and 7 in all editions apart from
1963 in which they are Plates 2 and 4) and one diagnostic plate (Plate 22 in all editions apart from 1963 in which it is Plate 15). The diagnostic plates feature two numerals, one designed to be invisible to protan observers and the other to deutan observers. For the diagnostic plate, spectra were sampled both from the protan numeral (Di.1; sample 5), and from the deutan figure (Di.2; sample 6). See Table 1 for a summary of the plates sampled.

All measurements except one were made using a PR655 spectrophotometer (Photoresarch, Chatsworth, CA), in a dark room, using an imitation daylight bulb (Solux, Rochester, New York, USA) in reference to a polytetrafluoroethylene white standard (Sphere Optics, Uhldingen, Germany). The remaining measurement was of one disc from transformation plate 1 of the 1975 edition, which was measured using a PR650 spectroradiometer (Photoresarch, Chatsworth, CA), under the same lighting conditions as previous measurements.

4.3.3 Observers
In total, eight observers were used in the modelling section of this investigation. For all sections not directly investigating the effect of severity of anomalous trichromacy, two observers were used. Deuteranomalous and protanomalous observers were constructed using a combination of the Smith and Pokorny (1975) cone fundamentals for the normal cone classes, and the DeMarco et al. (1992) fundamentals for the anomalous cone classes. The DeMarco et al. (1992) deuteranomalous observer (Figure 3, a) has a $\Delta \lambda_{\text{max}}$ of 5 nm, and the DeMarco et al. (1992) protanomalous observer has a $\Delta \lambda_{\text{max}}$ of 7 nm (Figure 3, c).
To investigate the effect of the severity of anomalous trichromacy (Section 4.4.3), six observers were simulated using a nomogram (Stockman & Sharpe, 2000) to model three severities each for deuteranomaly and protanomaly. The severity of anomalous trichromacy was modelled by adjusting the $\Delta \lambda_{\text{max}}$ of the two x-linked cone fundamentals. Severe anomalous trichromacy was modelled using a $\Delta \lambda_{\text{max}}$ of 3 nm, moderate anomalous trichromacy by a $\Delta \lambda_{\text{max}}$ of 6 nm and mild anomalous trichromacy by a $\Delta \lambda_{\text{max}}$ of 12 nm (Figure 3, b and d). These cone fundamentals were constructed using Stockman and Sharpe’s (2000) nomogram for simulating cone fundamentals of a given peak sensitivity. The simulated sensitivity as a function of log wavelength $\log_{10}(S(x))$ is calculated according to Equation 2, where $a = -188862.97$, $b = 90228.97$, $c = -2483.53$, $d = -6675.01$, $e = 1813.53$, $f = -215.18$, $g = 12.49$, and $h = -0.29$. Cone fundamentals with different values for $\lambda_{\text{max}}$ are created by shifting the template along the log frequency scale ($x = \log_{10}(\lambda) - \log_{10}(\lambda_{\text{max}}/558)$).

$$\log_{10}(S(x)) = a + bx^2 + cx^4 + dx^6 + ex^8 + fx^{10} + gx^{12} + hx^{14}$$


Pre-receptoral filtering was modelled using the macular pigment transmittance function used by Stockman, Sharpe and Fach (1999), and a lens transmittance function calculated for a 20-year-old observer using equations provided by Pokorny et al. (1987). Optical densities were estimated as 0.38 0.38, and 0.3 for L, M and S cones, respectively (Stockman and Sharpe, 2000). Scaling factors were applied before the pre-receptoral
filters to replicate the relative sensitivities of the Stockman and Sharpe (2000) fundamentals for the 20-year-old observer.

Figure 3. Cone sensitivity functions for anomalous trichromats used in the model. (a) Deuteranomal with normal trichromatic L and S cone sensitivity functions (Smith Pokorny, 1975) and an anomalous L’ cone sensitivity function (DeMarco et al., 1992). (b) Cone fundamentals for three severities of deuteranomaly created using a nomogram (Stockman & Sharpe, 2000). Each observer has normal trichromatic L (red) and S (blue) cone sensitivity functions and one of the three anomalous sensitivity functions (green), resulting in a Δλ_{max} of 3 nm, 6 nm or 12 nm. (c) Protanomal with normal trichromatic M and S cone sensitivity functions (Smith and Pokorny, 1975) and an anomalous M’ cone sensitivity function (DeMarco et al., 1992). (d) Cone fundamentals for three severities of protanomaly created using a nomogram (Stockman & Sharpe, 2000). Each observer has normal trichromatic M (green) and S (blue) cone sensitivity functions and one of the three anomalous M’ sensitivity functions (green), resulting in a Δλ_{max} of 3 nm, 6 nm or 12 nm. Insets indicate Δλ_{max}. 
4.2.4 Illuminants
Spectra for Blue Daylight and Yellow Daylight were taken from the high and low temperature extremes of the Granada Daylights dataset (Hernández-Andrés et al., 2001). LED, Halogen and Imitation Daylight spectra were recorded using a PR655 spectroradiometer (Photoresearch, Chatsworth, CA, USA), in reference to a polytetrafluoroethylene (PTFE) white standard (Sphere Optics, Uhldingen, Germany). The fluorescent spectrum from a Philips TL-D bulb, was obtained from an online dataset (Aphalo, 2015, mv.helsinki.fi) and converted from photons to energy. The D50 and D65 spectra are standard illuminants obtained from Appendix 5 of “Measuring Colour” (R. W. G. Hunt & Pointer, 2011).

Figure 4. Illuminant spectral power distributions. (a) natural illuminants; Blue Daylight and Yellow Daylight, (b) incandescent illuminants; Imitation Daylight and Halogen, (c) standard illuminants; D50 and D65, (d) narrowband illuminants; TL-D Fluorescent and LED.

4.2.5 Predicting signals available to anomalous trichromats for Ishihara plates
We estimated the cone opponent signals available to anomalous trichromats viewing each plate. Signals were estimated separately for each cone opponent channel (anomalous equivalents of L/(L+M) and S/(L+M)). The available signal is defined using a difference (Δ) metric, which refers to the absolute difference between the observer-specific
chromaticities of the pseudoisochromatic figure and the observer-specific chromaticities of the background, e.g. $|\Delta (L/(L'+L))|$. If the chromaticities of the figure discs do not overlap in range with those of the ground discs, there are 3 defined chromatic signals per plate (Figure 5, a & b), which are the absolute differences between the observer-specific chromaticities of the 3 discs within the figure (numeral) and the nearest observer-specific chromaticity of a ground disc. Any chromaticities of figure discs that fall within the range of the chromaticities of ground discs are not expected to confer a useable signal and were removed from all further calculations (Figure 5, c), resulting, for some plate-observer combinations, in only two modelled ‘signals’ for the plate instead of three. The signals modelled represent the chromatic information available to discriminate portions of the plate designed to be indiscriminable, and thus, a greater signal equates to a weaker plate, in that a greater signal should potentially contribute to a greater number of false negative readings.

Figure 5. Model of the cone opponent signals available to anomalous trichromats for Ishihara plates. (Left) Three discs selected from the part of a transformation plate numeral that is designed to be pseudoisochromatic with the surround for CVD observers, and three discs selected from the ground. (Right) The chromatic signals available that may
allow anomalous trichromats to identify the numeral are calculated as the observer-specific differences in chromaticity between each figure disc and the nearest ground disc. In scenario (a) the figure is redder than the ground, and in scenario (b) the figure is greener than the ground, but both will give rise to positive values for the absolute difference, e.g. $|\Delta(L/(L'+L))|$. In scenario (c) the range of chromaticities from the group of figure discs overlaps the range for the ground discs. In this instance, the available signal is calculated as the absolute difference in observer-specific chromaticity from the nearest ground disc to the remaining figure discs.

4.3 Modelling investigation: Results

4.3.1 Effect of plate

Figure 6. Cone-opponent signals predicted for anomalous trichromats viewing Ishihara Plates. Anomalous $|\Delta(L/(L+M))|$ signals are represented on the Y axis to the right, including protanomalous $|\Delta(M/(M+M'))|$ and deuteranomalous $|\Delta(L/(L'+L))|$. 
Anomalous $S/(L+M)$ signals are represented on the $Y$ axis to the left, including protanomalous $|\Delta(S/(M+M'))|$ and deuteranomalous $|\Delta(S/(L'+L))|$. The greater the signal difference, the more information is available to the observer to discriminate a figure designed to be indiscriminable, and the weaker the test. Coloured points indicate individual signals, wide bars 95% confidence intervals, the black line indicates the mean.

|               | Deutan $|\Delta(L/(L'+L))|$ | Protan $|\Delta(M'/(M+M'))|$ |
|---------------|----------------------------|----------------------------|
|               | $M$  | $SD$ | $M$  | $SD$ |
| Va.1          | 0.0061 | 0.0011 | 0.0097 | 0.0024 |
| Va.2          | 0.0085 | 0.0010 | 0.0139 | 0.0019 |
| Tr.1          | 0.0058 | 0.0009 | 0.0091 | 0.0018 |
| Tr.2          | 0.0055 | 0.0008 | 0.0091 | 0.0015 |
| Di.1          | 0.0104 | 0.0011 | 0.0162 | 0.0018 |
| Di.2          | 0.0086 | 0.0012 | 0.0124 | 0.0024 |

Table 2. a) Mean predicted $|\Delta(L/(L'+L))|$ and $|\Delta(M'/(M+M'))|$ signals for each plate averaged across editions ($M$), and standard deviations ($SD$). $P$-values from post hoc (Tukey) tests comparing plates on b) the predicted $|\Delta(L/(L'+L))|$ signals available to deuteranomalous observers, and c) the predicted $|\Delta(M'/(M+M'))|$ signals available to protanomalous observers. *$p<.05$, **$p<.01$, ***$p<.001$.

To test the effect of plate on the mean chromatic signal available to anomalous trichromats, 1-way ANOVAs with 6 levels for plate were conducted separately for deuteranomalous $|\Delta(L/(L'+L))|$ and protanomalous $|\Delta(M'/(M+M'))|$ trichromats, including all editions, under the imitation daylight illuminant. The ANOVA revealed a significant main effect of plate for both deuteranomalous ($F(5,36)=25.495$, $p<.001$) and protanomalous observers ($F(5,36)=14.846$, $p<.001$). Post hoc Tukey tests revealed that aside from a few exceptions, the difference between pairs of plates is significant (Table 2). The predicted chromatic signals available to anomalous trichromats for each plate
modelled are shown in Figure 6. The figure shows that Di.1 contributes the highest predicted $|\Delta (L/(L'+L))|$ signals ($M=.0104$, $SD=.0011$, Table 2), and highest $|\Delta (M'/(M+M'))|$ signals ($M=.0162$, $SD=.0018$). Post hoc Tukey tests revealed that Di.1 generated significantly greater predicted signals than all other plates for the deuteranomalous observer, and all plates aside from Va.2 for the protanomalous observer (Table 2). Both transforming plates (Tr.1 $M=.0058$ $SD=.0009$; Tr.2 $M=.0055$ $SD=.0008$) are predicted to contribute significantly smaller $|\Delta (L/(L'+L))|$ signals than both diagnostic plates (Di.1 $M=.0104$ $SD=.0011$; Di.2 $M=.0086$ $SD=.0012$) and Va.2 ($M=.0085$ $SD=.001$). Both transforming plates and Va.1 therefore are predicted to be the most effective for identifying deuteranomalous observers as they should be least prone to generating false negative readings (Figure 6, Table 2). The same trend is true for protanomalous observers, where both transforming plates and Va.1 are predicted to generate significantly smaller signals (Tr.1 $M=.0091$ $SD=.0018$; Tr.2 $M=.0091$ $SD=.0015$; Va.1 $M=.0097$ $SD=.002$) than both diagnostic plates (Di.1 $M=.0162$ Di.2 $M=.0124$; Table 2).
4.3.2 Effect of edition

Figure 7. Variation in predicted cone opponent signals between editions. Anomalous trichromatic $|\Delta(L/(L+M))|$ signals are represented on the Y axis to the right, including protanomalous $|\Delta(M'/(M+M'))|$ and deuteranomalous $|\Delta(L/(L'+L))|$. Anomalous $|\Delta(S/(L+M))|$ signals are represented on the Y axis to the left, including protanomalous $|\Delta(S/(M+M'))|$ and deuteranomalous $|\Delta(S/(L'+L))|$. The greater the predicted signal difference, the greater the predicted information available to anomalous trichromats to discriminate a figure designed to be indiscriminable, and the weaker the test. Coloured points indicate individual predicted signals, wide bars indicate 95% confidence intervals, the black line indicates the mean.
The effect of variation between editions was investigated using one-way ANOVA, with 7 levels for edition, including mean chromatic signal from each plate, with the default illuminant, imitation daylight. Separate tests were run for protanomalous and deuteranomalous predicted signals. The test identified no significant effect of edition on either deuteranomalous \( |\Delta (L/(L'+L))| \) signal (F(6,35)=0.499, p=0.805), or protanomalous \( |\Delta (M'/(M+M'))| \) signal (F(6,35)=1.289, p=.288). All predicted chromatic signals from all plates are presented per edition in Figure 7. Post hoc Tukey tests revealed that the 1991 edition is predicted to confer significantly smaller anomalous \( |\Delta L/(L+M)| \) signals than the 1963 edition for both protanomalous (M=.005, SE=.00093, p<.001) and deuteranomalous (M=.002, SE=.00053, p=0.017) observers (Table 3, Figure 7). The 1991 edition is also predicted to confer significantly smaller anomalous \( |\Delta L/(L+M)| \) signals than the 1981 edition for deuteranomalous observers (M=.002, SE=.00053, p=0.018) but not for protanomalous observers (M=.003, SE=.00093, p=0.058). For protanomalous
observers, the 1991 edition is also predicted to confer smaller signals than the 1975 edition (M=.004, SE=.00093, p=.005).

4.3.3 Effects of type and severity of anomalous trichromacy

Figure 8. Variation in predicted signals between editions for three severities of anomalous trichromacy, defined by their Δλ\text{max}, including a) mild anomalous trichromacy (12 nm Δλ\text{max}), b) moderate anomalous trichromacy (6 nm Δλ\text{max}), and c) severe anomalous trichromacy (3 nm Δλ\text{max}). The anomalous equivalent of |Δ(L/(L+M))| is plotted on the Y axis to the right, for protanomals (orange) and deuteranomals (green), and bars indicating the 95% confidence interval. The anomalous equivalent of |Δ(L/(L+M))| is plotted the left Y axis, for deuteranomals (blue) and protanomals (purple).
Table 4. Mean predicted chromatic signals (M) per edition for each severity of anomalous trichromacy for a) deuteranomals and b) protanomals, and the standard deviations (SDs).

The simulated protanomalous and deuteranomalous observers based on the DeMarco et al. (1992) cone fundamentals used for Sections 4.4.1 and 4.4.2 have a 2 nm difference in $\Delta \lambda_{\text{max}}$ – protanomals have a $\Delta \lambda_{\text{max}}$ of 7 nm, while deuteranomals have a $\Delta \lambda_{\text{max}}$ of 5 nm. Predicted protanomalous $|\Delta(M'(M+M'))|$ signals are subsequently consistently greater than the deuteranomalous $|\Delta(L'(L'+L))|$ signals, evident in the results shown in Tables 2 and 3, and Figures 6 and 7. To test the effect of type of anomalous trichromacy on the predicted chromatic signals available to the two DeMarco et al. observers, a 2-way ANOVA was conducted with observer type (protanomalous and deuteranomalous) as one factor and plate as a second factor. Chromaticities from all editions were included in the analysis, modelled under imitation daylight illuminant. The ANOVA identified a significant main effect of observer ($F(1,240)=192.968$, $p<.001$). There was also a significant main effect of plate ($F(5,240)=42.527$, $p<.001$), but no significant interaction.

To identify the impact of the severity of anomalous trichromacy on the predicted chromatic signals available from the Ishihara plates test, a two-way ANOVA was conducted with factors for severity, modelled using three levels of $\Delta \lambda_{\text{max}}$, and type (protanomalous and deuteranomalous). Observers were modelled using cone fundamentals based on a nomogram (Section 4.3.3). Chromatic signals were modelled with the default illuminant, imitation daylight, including all samples from all plates in all editions. The ANOVA revealed that both severity and type had significant main effects.
Severity (F(2,246)=340.904, p<.001) had a larger impact on predicted signals than type (F(1,246)=25.381, p<.001). There was no significant interaction. As expected, predicted signals decreased with severity (Table 4). Predicted signals were larger for deuteranomalous than protanomalous for observers based on the nomogram (Table 4). This finding was opposite to the finding from the model based on the DeMarco et al. cone fundamentals where predicted signals were greater for protanomals than deuteranomals but is attributable to the larger $\Delta \lambda_{\text{max}}$ for protanomals than deuteranomals with the DeMarco et al. (1992) cone fundamentals.

### Table 5. Results of two two-way ANOVAs testing the effects of severity of anomalous trichromacy and test edition on predicted deuteranomalous $|\Delta(L/(L'+L))|$ signals (a) and protanomalous $|\Delta(M'/(M+M'))|$ signals (c) available from Ishihara plates, with post hoc Tukey tests (b and d).

To identify whether the severity of anomalous trichromacy had a different impact on predicted chromatic signals between editions a two-way ANOVA was conducted with three levels for severity and seven levels for edition. All predicted signals from all plates were included, modelled with imitation daylight. Separate ANOVAs were run for protanomalous $|\Delta(M'/(M+M'))|$ and deuteranomalous $|\Delta(L/(L'+L))|$ observers. The ANOVAs revealed a significant main effect of severity for both deuteranomalous
(F(2,357)=379.36, p<.001, Table 5, a) and protanomalous observers (F(2,357)=371.873, p<.001, Table 5, b). The impact of severity of anomalous trichromacy on anomalous $|\Delta (L/(L+M))|$ and anomalous $|\Delta (S/(L+M))|$ can be seen in Figure 8. Mild anomalous trichromats are predicted to receive significantly greater signals than the moderate anomalous trichromats, who in turn are predicted to receive significantly greater signals than the severe anomalous trichromats (Tables 5, b and d). There was a significant main effect of edition (F(6,357)=3.84, p<.001). However, there was no significant interaction between severity and edition, indicating that severity of anomalous trichromacy does not cause different predicted effects on signals between editions.

These results show that the severity of anomalous trichromacy has a great impact on the predicted $|\Delta (L/(L+M))|$ signals available, but two-way ANOVAs with severity and edition as factors for anomalous $\Delta (S/(L+M))$ signals showed no significant main effect of severity, for either deuteranoms (F(2,105)=.046, p=.955) or protanoms (F(2,105)=.136, p=.873), indicating that as the severity of anomalous trichromacy increases there is no significant change in signals available in the S/(L+M) channel.
4.3.4 Effect of illuminant

Figure 9. Variation in cherry/teal cone opponent signal by illuminant, with deuteranomalous $\Delta(L/L'+L)$ represented in green and protanomalous $\Delta(M'/M+M')$ in red. Signal is presented for three severities of anomaly, defined by their $\Delta\lambda_{\text{max}}$, including a) mild anomalous trichromacy (12 nm $\Delta\lambda_{\text{max}}$), b) moderate anomalous trichromacy (6 nm $\Delta\lambda_{\text{max}}$), and c) severe anomalous trichromacy (3 nm $\Delta\lambda_{\text{max}}$). Horizontal dashed lines indicate the upper and lower confidence intervals of signal with imitation daylight, the illuminant used as the default elsewhere in the paper. Points indicate mean signal per edition, vertical line indicating range and bars indicating the 95% confidence interval.
Table 6. Variation in a) the $\Delta (L/(L'+L))$ signal and b) the $\Delta (M'/(M+M'))$ signal under 8 illuminants for three levels of anomaly severity. Mean (M) and standard deviation from mean (SD) are given for signals averaged across plates and editions.

To test the effect of illuminant on the predicted $\Delta (L/(L'+L))$ and $\Delta (M'/(M+M'))$ signals available in the Ishihara Plates test we performed two-way ANOVAs with factors for illuminant and severity, with separate tests for deuteranomals and protanomals. The mean signal per plate was included from all plates in all editions, modelled for each of the eight illuminants. A significant main effect of illuminant both for deuteranomals (F(7,984)=9.004, p<.001) and protanomals (F(7,984)=45.25, p<.001) was identified. There was also a significant main effect of severity for both deuteranomals (F(2,984)=1395.07, p<.001) and protanomals (F(2,984)=1307, p<.001). There was a significant interaction between severity and illuminant for protanomals (F(14,984)=5.053, p<.001) but not deuteranomals (F(14,984)=1.539, p=0.091). Post hoc Tukey tests (Table 7, b and d), indicate that more of the illuminants gave rise to significantly different signals for the protanomalous observer (Table 7, b) than deuteranomalous observers (Table 7, d).
Table 7. Two ANOVAs comparing variation with severity of anomaly and illuminant, of deuteranomalous $\Delta(L/(L'+L))$ signal (a, b, c) and protanomalous $\Delta(M'(M+M'))$ signal (d, e, f) available in Ishihara plates tests, including the $p$ values from post hoc Tukey tests averaging across severity, and simple main effect of illuminant for each severity of anomaly.

The impact of individual illuminants on predicted colour signals is shown in Figure 9 and Table 6. Compared to the imitation daylight illuminant, the majority of illuminants produced smaller predicted signals for both deuteranomalous and protanomalous observers, with the exception of halogen and fluorescent, which produced significantly greater predicted signals than any other illuminant for both deuteranomalous and protanomalous observers (all pairwise comparisons including the halogen illuminant were significant in post hoc Tukey tests, Table 7, b and d). For deuteranomals, LED produced the smallest signals, but for protanomals, the illuminant producing the smallest signals was blue daylight, which provided significantly smaller signals than all the other illuminants (Table 6, Table 7, d).
4.4 Behavioural investigation: Methods

A behavioural experiment was carried out to identify whether the variation between editions of the Ishihara Plates test in the colour signals available to anomalous trichromats identified by the model could predict the number of false-negative plate readings made by CVD observers.

4.4.1 Apparatus
The test was performed in a custom-built viewing box housing 3 imitation daylight bulbs, outputting a total of 2100 lm (Solux, Rochester, New York, USA). The spectral power distribution of the imitation daylight bulbs is shown by the black curve in Figure 4(a), an illuminant based on a halogen bulb with a filter attenuating longer wavelengths. The apparatus shielded the majority of daylight ambient illumination, but there was some ambient illumination from the surroundings. Participants viewed test plates at a 45-degree angle, at a distance of 65 cm.

4.4.2 Participants
Recruitment was via screening for CVD carried out using a shortened Rayleigh match procedure with an anomaloscope (Okulus, Wetzlar, Germany). In the shortened procedure 3 matches were gathered where adjustments were restricted to the ratio of red to green in the matching field – adjustments to the luminance of the orange test field were not allowed. Participants were asked to “turn the dial until the colours match”. The starting position of the trials alternated between the two extremes of the normal matching range. If a participant accepted any matches outside the normal range, a full test procedure was carried out requiring 5 further matches. Classifications based on the full
procedure identified 11 deuteranomals, 9 protanomals, 3 extreme deuteranomals, 3 extreme protanomals, 6 deuteranopes and 3 protanopes. Extreme anomalous trichromacy was defined as a wide matching range that includes typical matches accepted by both simple anomalous trichromats and normal trichromats (Pokorny et al., 1982). The three classes of CVD observer referred to in the behavioural portion of this investigation (Section 4.5) refer to those identified using the anomaloscope (anomalous trichromats, extreme anomalous trichromats and dichromats), and must not be conflated with the three severities of anomalous trichromacy ($\Delta \lambda_{\text{max}}$ of 3, 6 and 12) referred to in the modelling section of this investigation (Sections 4.3 and 4.4).

All 35 participants found to have CVD took part in the full study. 26 control adults found to have normal colour vision were also recruited after also taking part in the full anomaloscope procedure. Participants were from the Sussex University student population. The CVD group had a mean age of 20.91 (STD 2.97) and was comprised of 33 males and 2 females. The control group had a mean age of 21.26 (STD 3.64) and was gender matched to the CVD group.

All participants both for the screening test and the full study provided written informed consent. Ethical approval for the study was granted by the University of Sussex Science and Technology Cross-Schools Research Ethics Committee (ER/LS487/7).

4.4.3 Procedure
Seven editions of Ishihara Plates test were administered manually in a pseudo-random order. Verbal responses were recorded to the 24 numeric plates of the 6 editions of the

4.5 Behavioural investigation: Results

Figure 10. Ishihara Plates test error rate for 6 CVD observer groups when completing 7 editions of Ishihara Plates test. Error rate is number of errors made divided by number of plates in the test, to account for the shorter 1963 Edition. Points indicate individual participant error rates, bars indicate the 95% confidence intervals, and the black points indicate mean error rates.
Table 8. Mean and standard deviation of error rate for each of the CVD observer groups (DA: deuteranomals, PA: protanomals, EDA: extreme deuteranomals, EPA: extreme protanomals, D: deuteranopes, P: protanopes), for each edition of Ishihara Plates test.

<table>
<thead>
<tr>
<th>Year</th>
<th>DA M</th>
<th>DA SD</th>
<th>PA M</th>
<th>PA SD</th>
<th>EDA M</th>
<th>EDA SD</th>
<th>EPA M</th>
<th>EPA SD</th>
<th>D M</th>
<th>D SD</th>
<th>P M</th>
<th>P SD</th>
</tr>
</thead>
<tbody>
<tr>
<td>1963</td>
<td>0.81</td>
<td>0.22</td>
<td>0.51</td>
<td>0.42</td>
<td>0.96</td>
<td>0.07</td>
<td>0.94</td>
<td>0.00</td>
<td>0.89</td>
<td>0.11</td>
<td>0.88</td>
<td>0.17</td>
</tr>
<tr>
<td>1975</td>
<td>0.74</td>
<td>0.21</td>
<td>0.49</td>
<td>0.43</td>
<td>0.89</td>
<td>0.02</td>
<td>0.93</td>
<td>0.05</td>
<td>0.82</td>
<td>0.13</td>
<td>0.92</td>
<td>0.07</td>
</tr>
<tr>
<td>1981</td>
<td>0.77</td>
<td>0.20</td>
<td>0.52</td>
<td>0.46</td>
<td>0.90</td>
<td>0.10</td>
<td>0.99</td>
<td>0.02</td>
<td>0.78</td>
<td>0.11</td>
<td>0.92</td>
<td>0.14</td>
</tr>
<tr>
<td>1991</td>
<td>0.84</td>
<td>0.22</td>
<td>0.55</td>
<td>0.43</td>
<td>0.88</td>
<td>0.07</td>
<td>0.99</td>
<td>0.02</td>
<td>0.88</td>
<td>0.12</td>
<td>0.92</td>
<td>0.08</td>
</tr>
<tr>
<td>2010</td>
<td>0.79</td>
<td>0.19</td>
<td>0.55</td>
<td>0.45</td>
<td>0.85</td>
<td>0.06</td>
<td>1.00</td>
<td>0.00</td>
<td>0.81</td>
<td>0.04</td>
<td>0.93</td>
<td>0.09</td>
</tr>
<tr>
<td>2013</td>
<td>0.81</td>
<td>0.20</td>
<td>0.56</td>
<td>0.44</td>
<td>0.88</td>
<td>0.08</td>
<td>0.97</td>
<td>0.02</td>
<td>0.84</td>
<td>0.12</td>
<td>0.94</td>
<td>0.06</td>
</tr>
<tr>
<td>2017</td>
<td>0.79</td>
<td>0.21</td>
<td>0.53</td>
<td>0.46</td>
<td>0.88</td>
<td>0.00</td>
<td>0.96</td>
<td>0.04</td>
<td>0.88</td>
<td>0.16</td>
<td>0.93</td>
<td>0.09</td>
</tr>
</tbody>
</table>

For each observer and each edition an ‘error’ rate was calculated as the mean number of errors per plate (Figure 10), with mean error rates for deuteranomals (0.74-0.84 across editions) shown to be higher than mean error rates for protanomals (0.49-0.56, Table 8). Differences in the error rates made between observer groups were investigated using a two-way ANOVA with two levels for CVD type (protan and deutan) and three levels of CVD severity (anomalous trichromat, extreme anomalous trichromat and dichromat), combining results from all test editions. The ANOVA revealed no significant main effect of CVD type (F(1,239) = 1.02, p = 0.314) a significant main effect of severity (F(2,239)=27.0, p<.001), and a significant interaction (F(2,239) = 13.6, p < 0.001). Post hoc Tukey tests revealed that there were significantly fewer errors by protanomalous observers than by all other observer groups. This group difference is likely caused by the presence of 4 unusually mildly protanomalous observers in the protanomalous group (Figure 11).

A one-way ANOVA was conducted to test the impact of edition on error rate, combining all observers and all plates. There was no significant effect of edition (F(6)=.177,
This suggests that the predicted variation in chromatic signal between editions (Section 4.4.2) was not sufficient to influence error rate across all CVD observers completing the test. Variation in number of errors between editions (M=7.714, SD=2.217) was not sufficient to alter classification, apart from for four mildly protanomalous observers who did not meet the standard screening threshold of three errors for one or more editions (Figure 11). Although the 1975 edition misclassified all 4 mild protanomals with a fail criterion of 3 errors, all the other editions correctly identified at least 1 mild protanomal. This indicates that there could be some differences between editions in their ability to identify very mild cases of anomalous trichromacy.

![Figure 11](image)

*Figure 11. Errors made by 4 mild protanomals who were below diagnostic threshold of 3 errors for at least 1 edition. Each colour indicates a protanomalous observer, bars that fall below the red line were observers who would be falsely classified as normal trichromats.*

The relationship between the predicted chromatic signals available for a plate and errors for that same plate was tested using a Spearman correlation. Δ(L/(L’+L)) signals for
the nomogram-based deuteranomalous observer with a of $\Delta \lambda_{\text{max}}$ 6 nm (see Section 4.3.3) and $\Delta (M'/(M+M'))$ signals for an equivalent protanomaly. Modelled signals from all seven editions were included in the correlation, modelled with imitation daylight. Modelled signals were correlated with all the behavioural responses from anomalous trichromats to the five plates we included in the model (Section 4.3.2). There were negative correlations between the predicted signals for anomalous trichromats and the corresponding error rates for those plates ($\rho = -0.46, p = 0.005$ for deuteranoms; $\rho = -0.42, p = 0.02$ for protanoms). This suggests that as cone opponent signals available to anomalous trichromats increase, the error rate decreases, providing evidence that our model can predict performance on the Ishihara Plates test by anomalous trichromats. A scatter plot of observed error rates against modelled signals is provided in Figure 12, with the different plates and observer types identified by different markers.

Figure 12. The relationship between error rates of deuteranomalous (green markers) and protanomalous observers (red markers) and the anomalous $|\Delta(L/(L+M))|$ signal available.
from each plate modelled, including vanishing plates (indicated by dots), transformation plates (circles), and the diagnostic plate (asterisks).

4.6 General discussion

We have used our model of the chromatic signals available to anomalous trichromats for the Ishihara Plates test to make predictions about the test’s effectiveness for different viewing conditions and different observers. We found a significant negative correlation between the modelled chromatic signals available for particular plates and the average error rates by anomalous trichromats for those plates. As the sizes of predicted chromatic signals available for the vanishing portions of plates increase, the number of errors decreases, suggesting these chromatic signals are aiding CVD observers to give false negative readings. This correlation between the predicted signals and error rate supports the approach we have used in the model and validates its wider predictions.

For both types of CVD (protan and deutan) combined, severity had a far greater influence on predicted chromatic signals than all other factors, which is not surprising. Our model predicted that the influence of plate on the chromatic signals available to anomalous trichromats completing the Ishihara Plates test will be far greater than the influence of edition or illuminant choice. This is most pronounced for deuteranomalous observers, for whom edition had an effect size of $\eta^2=0.079$, and illuminant had an effect size of $\eta^2=0.06$, compared to the far larger effect size of $\eta^2=0.78$ for plate. For protanomalous observers, variation between editions gave an $\eta^2=0.181$, $\eta^2=0.22$ for illuminant, but plate again gave a greater effect size of $\eta^2=0.673$. These findings suggest
that the variation in cone-opponent signal between individual plates is far greater than the impact of variation between editions, or the influence of illumination.

Previous assessments of the Ishihara Plates tests have also identified chromatic variation between editions (Lee & Honson, 2003), and a possible effect of ageing on edition of the Ishihara plates test (Hyon et al., 2005). Our model predicted that differences in the chromaticities between the 7 editions tested would not be significant, and our behavioural study found no significant differences in error rate between editions. However, there was a suggestion in our result that different editions may have different abilities to detect mild anomalous trichromacy.

Our model’s predictions of the chromatic signals available for different plate types supports previous findings in the literature. Our model predicted that the weakest plates for identifying CVD would be the diagnostic plates, which have been previously found to have low sensitivity (Birch, 1997b; Katavisto, 1961; Lee & Honson, 2003; Pokorny et al., 1982).

We found that halogen illumination is predicted to provide the strongest chromatic signals in the vanishing portions of plates for both deuteranomalous and protanomalous observers, which could potentially lead to greater false negative readings. This concurs with findings that deutanomals make fewer errors under halogen or tungsten illuminants (Hardy et al., 1946; Higgins et al., 1978; Katavisto, 1961; Schmidt, 1952), and under spectrally manipulated illuminants with the highest energy at longer wavelengths (Tamura et al., 2017). Our model supports previous conclusions that fluorescent illuminants are unsuitable for colour vision testing (Pokorny et al., 1982), and supports
the use of blue-daylight or LED illuminant. Recommendations for best practice suggest using illuminants with a CCT of ~6500K, often via simulated daylight illuminants. However, our model predicted that the imitation-daylight-generated colour signals were not significantly different to the halogen tested, undermining its potential value as a substitute for Illuminant C. It is worth noting, however, that the imitation daylight bulb used was a filtered halogen bulb, and therefore likely to have a lower CCT than imitation daylights based on filtered fluorescent bulbs (Dain, 1998). Our model predicted that LED illuminants would provide the smallest colour signals for deuteranomals, but blue daylight would provide the smallest colour signals for protanomals, suggesting that these are most robust illuminants based on our findings.

We found that mean error rates for deuteranomals taking the Ishihara test (0.74-0.84 across editions) were higher than mean error rates for protanomals (0.49-0.56, Table 9). This may be due to the inclusion of four observers in our sample who were diagnosed as mildly protanomalous using the anomaloscope but did not reach the Ishihara screening threshold of three errors for some editions. Other research has also identified mild cases of anomalous trichromacy that do not reach the screening threshold of the Ishihara test (Birch, 1997b). It is likely that those with Rayleigh matches that are only mildly anomalous will have stronger chromatic signals at their disposal than those with more severe anomalous trichromacy. Our model predicts a strong relationship between chromatic signal strength and Δλ max. However, a recent meta-analysis has found the Δλ max accounts for only 15.2% of variance in red/green colour sensitivity (Bosten, 2019). It is therefore likely that other factors also influence anomalous observers’ perceptual capabilities on the Ishihara Plates test.
In conclusion, our study has identified that the chromatic signals available in the differences between ground points and vanishing points of Ishihara plates may contribute to false negative readings. Our model found illumination to have a significant effect on the available chromatic signal for anomalous trichromats, and we recommend that those screening should be carried out with LED or blue-daylight over halogen-based illuminants, including daylight simulators with a halogen base. Further work is needed to clarify the differences in susceptibility between the X-linked phenotypes, to excess chromatic signal available in pseudoisochromatic plates.
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