Conscious Perception of Illusory Colour

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Doctor of Philosophy

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Thesis Summary

Visual perception can be defined as the ability to interpret the pattern of light entering the eyes to form a reliable, useful representation of the world. A well-accepted perspective suggests that these interpretations are influenced by prior knowledge about the statistics of natural scenes and are generated by combining information from different cues. This thesis investigates how these processes influence our perception of two phenomena: afterimages and colour distortions across the visual field. Both are generated on the retina, do not represent meaningful properties of the physical world, and are rarely perceived during natural viewing. We suggested that afterimage signals are inherently ambiguous and thus are highly influenced by cues that increase or decrease the likelihood that they represent a real object. Consistent with this idea, we found that afterimages are enhanced by contextual edges more so than real stimuli of similar appearance. Moreover, afterimage duration was reduced by saccadic eye-movements relative to fixation, pursuit, and blinking, perhaps because saccades cause an afterimage to move differently to real object and thus provide a cue that the afterimage is illusory. Contextual edges and saccades were found to influence afterimage duration additively, although contextual edges dominated the probability of perceiving an afterimage more than saccades. The final part of the thesis explored the hypothesis that colour distortions across the retina, produced mainly by spectral filtering differences between the periphery and fovea, are compensated in natural viewing conditions. However, we did not find evidence of compensatory mechanisms in the two natural conditions tested, namely eye-movements (as opposed to surface movements) and natural spectra (as opposed to screen-based spectra). Taken together, the experiments in this thesis demonstrate that these 'illusory' phenomena perceived strongly in laboratory conditions but rarely during natural viewing, are useful tools to probe how perceptual decisions are made under different conditions.

Contents

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Chapter 1: General Introduction

Introduction

If you are new to vision science it is tempting to assume that the eyes and brain act like a rudimentary camera. Each moment in time is captured in a detailed array that reproduces the scene in its complete physical form. The error in this assumption is that the visual system is both more limited and more intelligent than this. More limited because we do not have the vast processing power that would enable every aspect of the scene to be encoded in perfect detail. More intelligent because the processing strategies we do have allow us to choose the most likely, and the most useful, perceptual interpretation at each moment. For instance, even at the lowest level of perceptual processing, the photoreceptors, we employ sophisticated compensatory mechanisms to help white remain broadly invariant across different illuminations (Webster, 2011). Only in recent years have we developed the software that allows cameras to perform a similar task instantaneously.

Low level processes on the retina go some way in transforming light patterns entering the eye into intelligible sensory information. The output of the retina remains fairly ambiguous, however, and further analysis is required to form a reliable representation of the world. Many processes have been suggested for how the brain disambiguates this pattern of retinal stimulation. This thesis focuses on three of these processes. First, many vision scientists believe that the machinery of the visual system adapts and calibrates to perform as optimally as possible based on natural scene statistics. Second, prior assumptions may be developed about the world that bias the interpretation of future visual events. Third, many different sensory cues could be combined when the representation is formed, possibly in a way that weights them based on their respective reliabilities. This is not to say that these processes are mutually exclusive, either conceptually or in terms of their underlying physiology. It is likely that all three are heavily influenced by perceptual experience and our sensory exploration of the world. However, the following overview separates them for clarity and because they are often studied in isolation.

1. Calibration of basic machinery

The visual system has adapted to perform better and better in the natural world over years of evolution and this calibration continues after birth through neural plasticity and learning. It has been said that 'the mind has been fit to the world' (Clifford & Rhodes, 2005), and examples of this 'fitting' are numerous in the literature on neural development. Cats reared in an environment of single orientated gratings display severe deficits to orientations perpendicular to the ones they have experienced (Blakemore & Cooper, 1970). Further, neurons in the visual cortices of cats are preferentially tuned to the single orientation to which they have been exposed. Similar findings have been reported for binocular depth, motion and colour constancy (Blake & Hirsch, 1975; Cynader & Chernenko, 1976; Sugita, 2004; Wiesel & Hubel, 1965). In colour vision, despite very different ratios of the three classes of photoreceptors on the retina, most people agree on the wavelengths that produce each of the four unique hues (Brainard et al., 2000). Further, it is likely that many aspects of visual processing have developed to efficiently code features based on the statistics of natural scenes (Felsen & Dan, 2005; Field, 1987; Geisler, 2008; Simoncelli & Olshausen, 2001). This literature demonstrates how insight about the mechanisms of the visual system may be best gained when it is studied in relation to the environment it has evolved and developed to represent.

2. Prior assumptions

Although the relentless cascade of sensory information entering the eyes may seem like an insurmountable amount for the brain to translate, it is made a little easier by the fact that many features of the world remain stable over time. For example, the light source predominantly comes from above and the world is stationary most of the time. It is likely that we form assumptions that reflect these stable characteristics of the world and use these assumptions to bias our interpretations of new sensory information (R. L. Gregory, 1997; Helmholtz, 1962). The illusion shown in Figure 1.1a demonstrates the prior assumption that that light source comes from above (Brewster, 1826; Ramachandran, 1988). Physically the circles are luminance gradients from light to dark or vice versa. What we perceive is illusory depth of either a convex or concave shape based on our assumption that the figure is illuminated from above. A further example, this time demonstrating our knowledge of luminance under different lighting conditions, is shown in Figure 1.1b (Purves & Lotto,

2011). The brown and orange square (within the grey circles) are physically the same, yet we perceive them as different because one is in shadow and the other is in light. The visual system deduces that the only way the luminance of these two squares could be the same under these different illuminant conditions, is if their lightness was different. Along with demonstrating that the brain uses prior knowledge to predict whether certain visual signals represent certain properties of the world, it also demonstrates how significant the surrounding context is in influencing these interpretations.

a   b
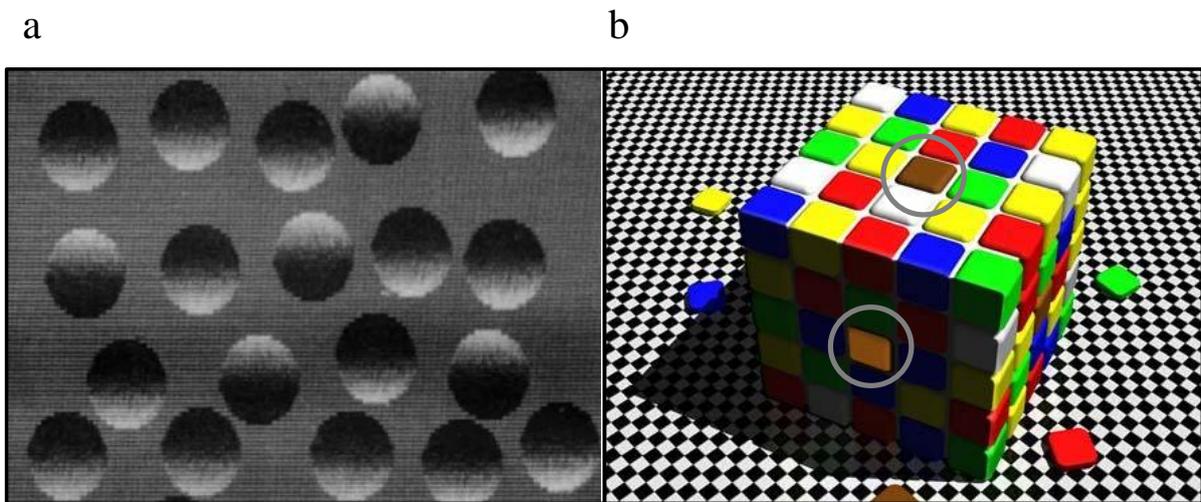
Figure 1.1. Illusions demonstrating the influence of prior assumptions about the world. *(a)* Physically all these circles are the same, apart from that in some the vertical luminance gradient is dark to light and in others it is light to dark. We perceive a strong perception of convex or concave depth because this fits best with the interpretation that the there is a single light source from above, as it usual in the natural world. Image taken from Ramachandran (1988) p.163. *(b)* The brown and orange squares (within the grey circles) are the same luminance but we perceive them as different because this is the best interpretation of equal luminance signals under different lighting conditions. Image from Lotto (2011).

3. Combination of sensory cues

Figure 1.1b demonstrates that the luminance of the surrounding context is used as a cue to influence the perceptual interpretation of the image. Often there are many different types of cues that could be used to interpret each perceptual event, both across and within the senses. It is probable that the brain rarely operates a 'winner takes all' rule, where one cue will dominate the perceptual interpretation in every situation. Rather, cues are combined in an advantageous, or statistically optimal, manner so that they are weighted in terms of their respective reliability. Thus, an optimal combination would result in a combined estimate of

the cues that has a lower variability than the individual cues by themselves (Ernst & Banks, 2002). A consequence of this is that our perceptual interpretations are not necessarily stable over time, but can be updated based on the most likely interpretation at any given moment. A classic example of this is the induced motion effect when sitting in a stationary train carriage while an adjacent train begins to move (Ernst & Bülthoff, 2004). Initially, the brain favours the interpretation that you are moving, thus producing an illusory sensation of self-motion. However over time, as evidence from vestibular cues accumulates, the brain switches its interpretation and perceives the adjacent train as moving.

Summary

The visual system is dynamic; it can learn from experience and adjust its interpretation based on the array of presented evidence. It is also likely that the more ambiguous the sensory information is, the more the visual system will rely on disambiguating cues and prior knowledge to drive the interpretation. Of course, the illusions in Figure 1.1 also demonstrate that the visual system does not always produce a veridical representation of what is physically present. In these cases, it is a little unfair to expect this given that these illusions are artificially designed to mislead the brain. A popular assumption in modern vision science is that these strategies are optimal most of the time in natural settings (Ernst & Bülthoff, 2004; Jazayeri & Movshon, 2006; Weiss, Simoncelli, & Adelson, 2002). This assumption could be taken to mean that we only see what is meaningful and what fits with our knowledge, assumptions, and lifelong learning of the natural world.

Rationale

The present thesis is concerned with two perceptual phenomena, both of which are distortions or artefacts of the retina and thus do not represent real world features, and yet are able to reach conscious perception. The experiments reported here aim to determine the conditions under which these phenomena are perceived. The findings are interpreted within the context of how different cues and prior experience influence our perception of these phenomena and how these strategies could have been learnt over time. Chapter 2 and 3 will explore luminance and colour afterimages, which arise when adaptation to a particular hue (or luminance) results in the subsequent illusory perception of its complementary hue (or opposite luminance). Chapter 4 is concerned with colour distortions across the visual field,

which are mostly due to macular pigment filtering short wavelength light at the fovea but not the periphery. What is interesting about both afterimages and colour variations across the visual field is that they are easy to demonstrate in controlled laboratory conditions and yet are often absent from our everyday visual experience. The mechanisms that generate these illusory perceptions serve useful ecological purposes (adaptation improves sensitivity in specific channels, macular pigment filters harmful short wavelength light), but the resultant perceptual consequences of these processes do not serve a useful purpose. The questions addressed by this thesis are thus: to what extent, and how, does the brain decide whether to perceive these phenomena or not. For afterimages, we are interested in whether different cues increase or decrease the likelihood that the afterimage signal represents a real object, and so determines the strength and duration of the afterimage perception. The cues we have focused on are the surrounding context (Chapter 2 and Chapter 3) and eye movements (Chapter 3), and how they are combined (Chapter 3). For colour distortions across the visual field, we were interested in the conditions that determine whether we perceive these differences or not. In particular, we have studied these variations under more natural viewing conditions, using natural spectra, and eye movements rather than surface movement (Chapter 4). The following introduction will discuss the past literature and theoretical framework for our perception of afterimages and colour variations across the retina.

Afterimages

"It is then not proper to say that an after-image has its seat either in the retina or in the brain; both retain an impress from the original stimulation, and though the persistence of the exciting substances in the retina is perhaps the more important element, yet the cortical impress plays a large part in determining the exact form in which the after-image shall appear."

- McDougall (1901, p. 377)

Unlike other types of aftereffects, it is probable that afterimages are formed from adaptation on the retina. From this we could conclude that afterimages are simply 'negative images', or perceptions arising from a shift in relative activity of cells early in the visual system. According to this view, the independent adaptation of photoreceptor cells and subsequent shifts in the activity of opponent processes are mainly responsible for the generation of

afterimage signals (Brindley, 1962; Craik, 1940; von Kries, 1970; Zaidi, Ennis, Cao, & Lee, 2012). The assumption follows that these signals are then processed by higher level visual areas equivalently to signals arising from any real stimulus (Barlow & Sparrock, 1964; Zaidi et al., 2012). However, as the quotation above from McDougall implies, the brain plays an important role in determining the form in which the afterimage will take. In practice this means that afterimages are unstable: under some conditions we perceive them strongly, under others we do not (Forde & Mackinnon, 1975; MacKinnon, Forde, & Piggins, 1969; Owen & Chalfant, 1970; Wade, 1978). An interesting example of the non-retinal modulation of afterimage perception is that afterimages that are generated separately on different eyes and are spatially displaced from each other tend to fluctuate in visibility in synchrony (A. H. Gregory & Arnold, 1971). Also, afterimages will disappear when a change in eye position projects them onto 'impossible' locations in space where objects are unlikely to be placed, such as on the side of the nose or the brow (Hayhoe & Williams, 1984).

In this thesis we argue that afterimage signals are fundamentally ambiguous, and this means that they are particularly influenced by cues that increase or decrease the likelihood that they represent a real object. Before discussing this theory further, we will review a short history of afterimages and describe how the different varieties may be generated.

Brief History of Afterimages

The term 'afterimages' was first coined by Purkinje in 1823 (Wade, 2000) but the phenomena had been studied for centuries before this under different names. Aristotle wrote about afterimages in his essay 'Parva Naturalia' (On Dreams):

'..after having looked at the sun or some other brilliant object, we close the eyes, then, if we watch carefully, it appears in a right line with the direction of vision (whatever this may be), at first in its own colour; then it changes to crimson, next to purple, until it becomes black and disappears' (Aristotle, Ross, & Smith, 1910).

Aristotle was followed in his interest by many of the key intellectual minds throughout history. Alhazen, Leonardo di Vinci, Boyle, Newton, Helmholtz, Robert and Erasmus Darwin, and many others all made observations about the nature of afterimages (Wade, 2000). Most used the sun for their adapting stimulus, and consequently, many became the victims of their own curiosity. Newton wrote that he shut himself in a dark room for three

days 'to recover the use of my eyes' because he had stared at the sun for too long (Wade, 2000, p.161). But it was Fechner, the founder of psychophysics, who suffered the greatest for his afterimage experimentation. His eyesight was so badly damaged he resigned from his academic position and became secluded until his sight gradually improved.

The reason why afterimages held such a dangerous interest for so many scientists and philosophers is perhaps best captured by Franz (1899):

'In the history of afterimages we seem to have an epitome of the interrelations of physics, physiology and psychology; and probably no other single phenomenon is so good an example of the growth of experiment and measurement in psychology'. (p. 1)

Franz's statement held true - over the next 100 years afterimages joined the growing interest in aftereffects and adaptation that was fuelled by their status as the 'psychophysicist's electrode' (Frisby, 1980). A sentiment also mirrored by the famous Mollon canon 'if it adapts, it's there' (Mollon, 1974, p.479). Afterimages have been, and continue to be, excellent tools to probe visual mechanisms. As stabilised retinal images, they have been used to explore eye movements and extra retinal signals (Grüsser, Krizicͺ, & Weiss, 1987; Heywood & Churcher, 1971), visual fading (McLelland, Ahmed, & Bair, 2009; Tulunay-Keesey, 1982), size constancy (Sperandio, Chouinard, & Goodale, 2012), binocular vision (Blake, Fox, & McIntyre, 1971; Tsuchiya & Koch, 2005; Wade, 1974), ways to distinguish attention from consciousness (Bachmann & Murd, 2010; van Boxtel & Koch, 2009) and many more. They have also been studied as phenomena in their own right. Yet, forming a complete understanding of afterimages is challenging because of the long, sporadic literature on them, the multiple forms they can take, and the numerous factors that influence their appearance and visability.

Types of afterimages and how they are generated

Afterimages have been known by many different names, including 'flight of colours', 'secondary images', 'quaternary images', 'insensitivity percepts', 'accidental colours' and 'ocular spectra'. There have been just as many explanations of how afterimages are generated as names for them and these explanations have evolved alongside our understanding of how colour and luminance are processed by the visual system. Unlike other types of aftereffects, such as tilt and motion, colour and luminance afterimages tend not to transfer intraocularly.

Furthermore, it is possible to generate an afterimage from a stimulus that is delivered to a pressure blinded eye (Cibis & Nothdurft, 1948, as cited in Craik, 1940; Weiskrantz, 2002). These findings are classically interpreted as evidence that afterimages are retinal in origin. We now know that there are probably two main types of retinal afterimages: those generated primarily by bleaching of the photoreceptor cells (here called 'photochemical' afterimages) and those due to mostly neural adaptation in opponent channels on the retina (here called 'ganglion' afterimages). Both photochemical and ganglion afterimages have fairly short times frames, ranging from seconds to minutes. A third type of afterimage, probably not of retinal origin, is longer lasting and can persist for hours, days or even years. These tend to be physiologically and perceptually very different to photochemical and ganglion afterimages. These three types of afterimages are now discussed separately in more detail.

Most early experiments are likely to have examined photochemical afterimages. These arise from bleaching of one or more of the three cone classes – those sensitive to short (S), medium (M) and long wavelength (L) light. In these experiments, the adapting stimuli tended to be of high intensity. Very early scientists used the sun, and then as technology progressed, photoflash generators were used. If the adapting stimulus is very intense, afterimages can progress thorough different colours before stabilising as either the bright or dark, a phenomenon observed by Goethe (Wilson & Brocklebank, 1955) and named by Helmholtz as the 'flight of colours' (Wade, 2000). Bright afterimages, or those as the same polarity as the adapting stimulus, are usually called positive afterimages. While dark afterimages, or those of opposite brightness to the adapting stimulus, are usually called negative afterimages. Whether a positive or negative afterimage is perceived depends on the background the afterimage is viewed against. If the background is darker than the afterimage, the afterimages will appear positive; if lighter than the afterimage, the afterimage will appear negative (Gerrits, Erning, & Eijkman, 1988; Kennard, Hartmann, Kraft, & Boshes, 1970; Virsu & Laurinen, 1977; Wilson & Brocklebank, 1955). The positivity or negativity of an afterimage can be immediately reversed simply by changing the luminance of the background or closing and opening the eyes (Carpenter, 1972; Matteson, 1965; Robertson & Fry, 1937). Afterimages can sometimes alternate between positive and negative even when the background remains constant (Gerrits et al., 1988; Otte, Valberg, & Spillmann, 2006; Taya & Ohinata, 2002). Negative afterimages are linearly related to the contrast of the adapting stimulus and will build up and decay exponentially (Kelly & Martinez-Uriegas, 1993). Afterimages will appear to increase

or decrease in size depending on the distance of the background it they are projected on to, a finding known as Emmert's law (Emmert, 1881; Liang Lou, 2007).

Photochemical afterimages tend to be relatively long-lasting, several minutes, as photo pigment takes a while to replenish (Mahroo & Lamb, 2004; Zaidi et al., 2012). Because of this, it has been suggested that the overall intensity of light matters more to the afterimage percept than the time over which the light is delivered (Brindley, 1959). Thus, even a brief light flash can generate a strong, long lasting afterimage by using up enough photo pigment.

The second type of afterimage arises from neural ganglion cell adaptation and can be generated by adaptors of a much lower intensities. Prolonged fixation (several seconds) of a low intensity adapting stimulus is required to produce a strong afterimage; a brief flash may be insufficient. Electrophysiological evidence in the macaque suggests that those neural afterimages are generated by adapted responses of retinal ganglion cells that are sensitive to the specific feature of the adapting stimulus (Zaidi et al., 2012). Retinal ganglion cells are part of the opponent system, where information about colour and luminance is relayed in three channels to higher visual areas. The L+M channel, or magnocellular pathway, sums input from L and M cones and carries low spatial, but high temporal, frequency luminance information. The L-M channel, or parvocellular pathway, carries chromatic information about the relative proportion of L and M cone excitation and also transfers high spatial frequency luminance information. The S channel, or koniocellular pathway, transmits information about the relative S cone activity compared to a combination of L and M cone activity. Prolonged fixation of short wavelength light will produce an adaptation signal in the S channel, resulting in the perception of physical grey being shifted towards a longer wavelength hue (yellow). Similarly, prolonged fixation of long wavelength light will result in a relative decrease of responding in of L channel relative to the M channel, resulting in an illusory perception of short wavelength light when grey is presented.

Figure 1.2 shows electrophysiological recordings from macaque ganglion cells as they undergo adaptation (Zaidi et al., 2012). Figure 1.2a shows an S channel retinal ganglion cell, which responds preferably to short wavelength (bluish) light, and is inhibited by long wavelength (yellowish) light. The spikes for this cell are plotted against time in seconds, as the macaque watches a slow screen modulation from grey-violet-grey (top graph) and grey-yellow-grey (bottom graph). The black line illustrates the recorded spikes rate from the cell, the blue line indicates the spike rate that would be expected if the cell did not adapt to the

short wavelength signal, and the red line indicates the spike rate predicted if the cell adapts to the short wavelength light. During the grey-violet-grey modulation, the cell spike rate decreases to baseline before physical grey is reached (adaptation), and continues to decrease in responding to below baseline, before gradually recovering. The fact that the cell is responding below baseline when grey is presented for the second time in the cycle may signify the underlying physiological representation of a yellow colour afterimage. The grey-yellow-modulation shows the opposite pattern of responding; the S+ cell is initially inhibited by the yellow modulation but recovers towards baseline before grey is reached. Figure 1.2b-c shows the same pattern of responding but for an M+ centre ganglion cells (b) and an L+M ganglion cell (c) as the macaque watches screen modulates isolating the poles of those two channels. Zaidi et al (2012) concluded that ganglion cells are the locus of the afterimage in their experiment, rather than the photoreceptors, because the adapting stimulus intensities were not sufficient to bleach a large quantity of photopigment.
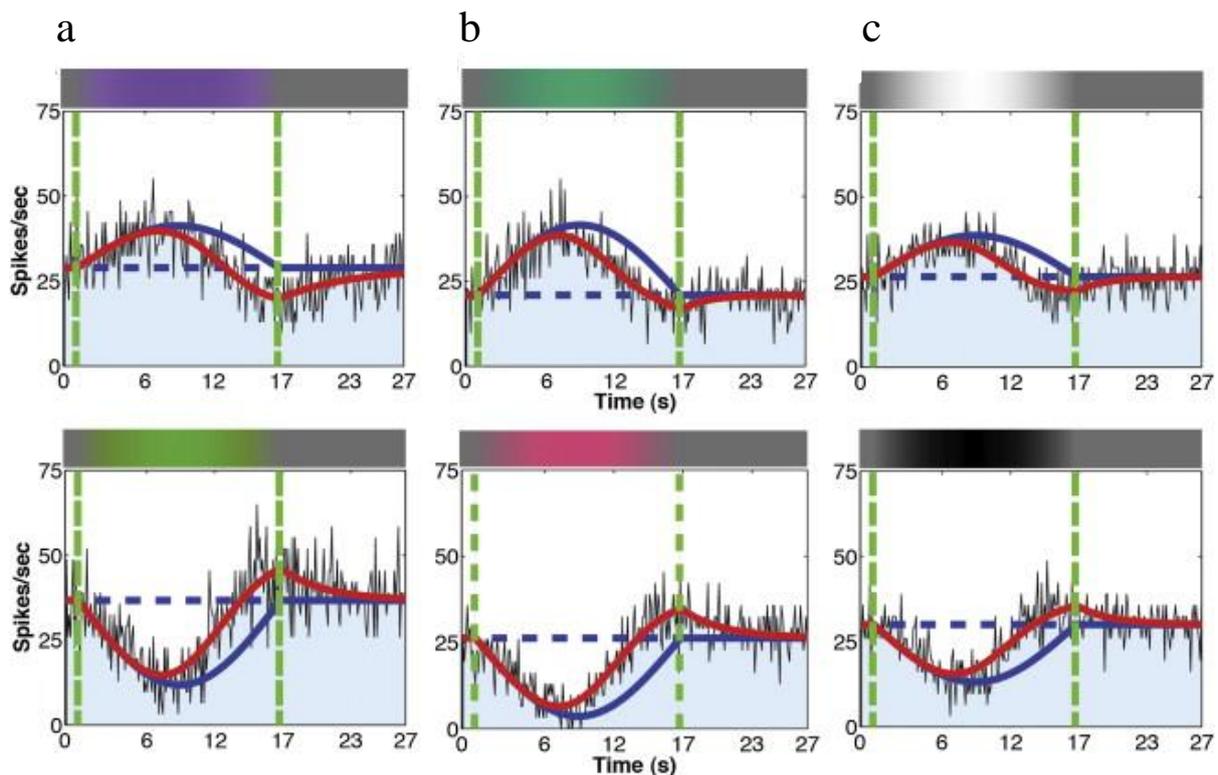
Figure 1.2. Electrophysiological recordings in a macaque showing ganglion cell activity (spike rate) underling the formation of a negative afterimage over time. *(a)* The coloured bar represents the physical stimulus presented. The spike rate of a ganglion cell that responds preferably to violet (black line) follows the spike rate predicted if adaptation occurs (red line) more than the predicted spike rate without adaptation (blue line). For both a stimulus that excites the cell (top graph) and inhibits it (bottom graph), the spike rate of the cell returns to baseline before physical grey is reached (e.g. while the hue is still presented) and then goes

past baseline when physical grey is reached. This relative decrease in specific channels following adaptation may underlie the perception of an afterimage complementary to the adapting stimulus when grey is presented. *(b)* Similar pattern of recordings shown for a ganglion cell that prefers M-cone responses and is inhibited by L-cone responses and *(c)* high luminance stimuli. Graphs taken from (Zaidi et al., 2012, p.222).

The third category of afterimages describes those with much longer time-scales than either photochemical or ganglion afterimages, both in terms of the length of adaptation required to produce them and the subsequent afterimage duration. Daily exposure to an environment biased with one particular colour, either through lenses, filters, or changes to the environmental illuminant, can produce very long-term colour aftereffects that sometimes do not recover after months of de-adaptation (Belmore & Shevell, 2008; Delahunt, Webster, Ma, & Werner, 2004; Eisner & Enoch, 1982; Neitz, Carroll, Yamauchi, Neitz, & Williams, 2002).

A famous example of long-lasting afterimages is the McCullough effect, where contingencies develop between colour and orientation (Jones & Holding, 1975; McCollough, 1965). Prolonged fixation of an orientated grating paired with a particular hue results in the illusory perception of the complementary hue when an achromatic grating of the same orientation is viewed subsequently (illusion shown in Figure 1.3). Thus, exposure to a red horizontal grating will later bias all perceptions of achromatic horizontal gratings towards green. One proposed explanation is that contingent afterimages reflect longer term recalibration and plasticity processes in the brain that aim to remove the biased pairing of one particular hue with one particular orientation, i.e. the visual system assumes the hue-orientation pairing represents an internal error (Dodwell & Humphrey, 1990). Photochemical/ganglion afterimages, on the other hand, represent transient changes in sensitivities in certain channels and do not produce long term changes. Of course, it may just be that there are more opportunities to 'de-adapt' from the photochemical/ganglion adaptation than hue-orientation contingencies (Vul, Krizay, & MacLeod, 2008). The ecological occurrences gratings similar in spatial frequency to the experimentally exposed grating are relatively low.

McCollough effects are probably due to adaptation or neural plasticity in areas beyond the retina (Barnes et al., 1999; McCollough, 1965). Although this thesis is primary concerned with afterimages of the retinal ganglion type, contingent aftereffects are excellent examples of the visual system's plasticity in response to the properties of sensory information. Also, they perhaps provide an example of how the visual system is driven to distinguish internal

errors from properties of the natural world in order to remove biases from our perceptual experience. However, henceforth, the word 'afterimages' is used here to describe percepts of a photochemical or ganglion origin.
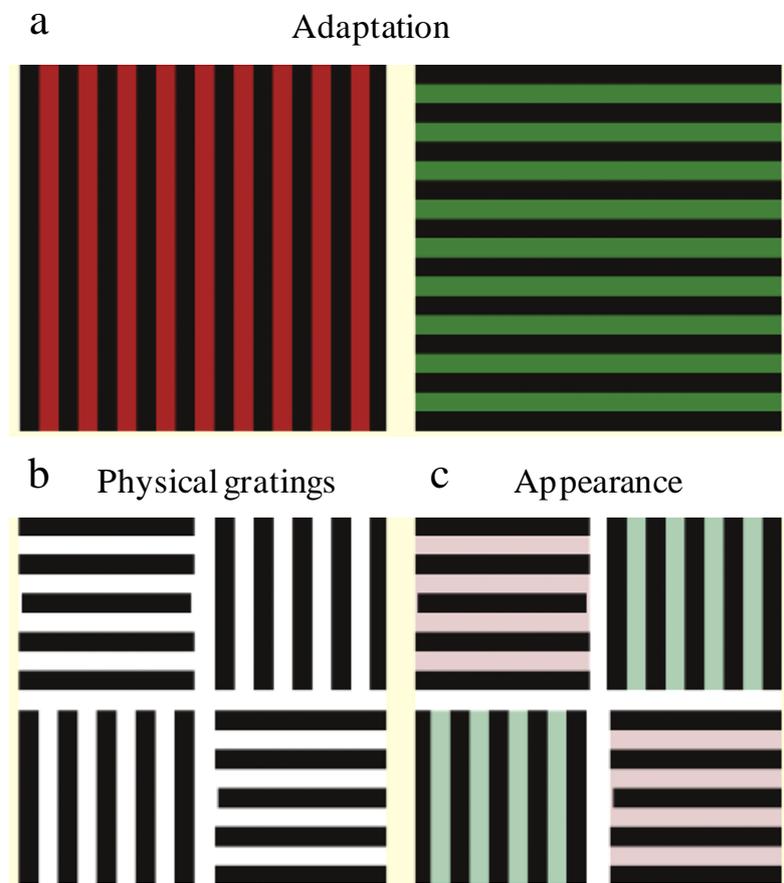
Figure 1.3. The McCullough effect. (*a)* An observer is adapted for some time to pairings of horizontal-green gratings and vertical-red gratings. *(b)* After adaptation, achromatic gratings are shown and (*c)* are now perceived as tinted in the opposite hue to the adaptation pairing: vertical gratings appear green, horizontal gratings appear red. Image adapted from (Thompson & Burr, 2009, p. R13.)

Influences on afterimage visibility

Afterimages are not often perceived in natural viewing. Occasionally a negative or positive afterimage may be perceived after staring at an intense light source, but afterimages from moderate light sources are much less frequent. One argument could be that we rarely fixate long enough to generate an afterimage, and the locations we fixate do not produce sufficient light to produce adaptation. During many daily activities this may be the case, however there are plenty of examples where fixation and adaptation intensities would be sufficient to

produce afterimage generating adaptation. For example, observations in our lab suggest that 100ms of adapting to a mid-luminance object (e.g. 30cd/m^2) is sufficient to generate a short, but visible, afterimage. This means that fairly short fixations of the bright square produced by a computer or television screen, or even the coloured boarders in the interfaces of many computer applications, may be frequently expected to generate an afterimage. This suggests that there is more to explaining our low frequency of afterimage perceptions than insufficient conditions for adaptation.

A next likely candidate for why we rarely perceive afterimages is that we simply do not notice or attend to them. As faint, blurry percepts, afterimages do not exemplify the properties of a typical attention grabbing stimulus. Effects such as inattentional blindness and change blindness demonstrate that we attend to very little of the visual information leaving the eye (Simons, 2000; Simons & Chabris, 1999; Simons & Rensink, 2005). Attention was held responsible for decreases in afterimage visibility by both Newton "..but when I ceased to intend my fancy upon them, they vanished again' (as cited in, Wade, 2000, p.165), and Goethe 'an attentive observer will see these appearances [afterimages] everywhere' (von Goethe & Eastlake, 1840, p. 22) However, it has been found that afterimages are salient enough to grab attention in visual search paradigms (Theeuwes & Lucassen, 1993). Attention towards an afterimage appears to decrease afterimage duration (Bachmann & Murd, 2010; Baijal & Srinivasan, 2009; L. Lou, 2001; Suzuki & Grabowecky, 2003), perhaps because top-down influence increases responses to the afterimage signal and hastens habituation processes. Although this thesis does not directly explore attentional effects on afterimage perception, this literature demonstrates that it is important to ensure attentional confounds are minimised when exploring other cues that modulate afterimage visibility.

Contextual edges and afterimages

One of the most striking modulators of afterimage visibility is the surrounding context they are viewed against. Popular afterimage illusions, such as the Spanish castle illusion (Sadowski, undated) and the recent illusion by van Lier, Vergeer, & Anstis (2009), demonstrate compelling effects of contextual modulators on afterimage visibility (Figure 1.4 shows the van Lier et al illusion). In these illusions, afterimages embedded in a consistent

context (usually a luminance edge or contour) are unequivocally visible, yet without such context they are much less visible, or even invisible.

Previous psychophysical and electrophysiological research has demonstrated that luminance or chromatic edges are also important in facilitating the perception of, and cellular responses to, physical chromatic stimuli to some extent (S. H. Friedman, Zhou, & von der Heydt, 2003). Perceptually, luminance contrasts (contours and pedestals) facilitate detection and discrimination of physical chromatic stimuli (Chaparro, Stromeyer Iii, Kronauer, & Eskew Jr, 1994; Cole, Stromeyer III, & Kronauer, 1990; Eskew Jr, Stromeyer Iii, & Kronauer, 1994; Gowdy, StromeyerIii, & Kronauer, 1999; Gur & Akri, 1992; Hilz & Cavonius, 1970; Hilz, Huppmann, & Cavonius, 1974; Montag, 1997; Mullen & Losada, 1994). In particular, a flashed suprathreshold luminance pedestal or contour (ring) facilitates detection of a coincident chromatic target (Chaparro et al., 1994; Cole et al., 1990; Eskew Jr et al., 1994). Additionally, weak, blurry chromatic signals spread ('fill-in/out') until they reach a luminance edge (von der Heydt, Friedman, & Zhou, 2003). A demonstration of this process can be seen in the watercolour and Boynton illusions (Mollon, 1995; Pinna, Brelstaff, & Spillmann, 2001). At a physiological level, orientation selectivity and heightened responses to edges are common features of visual cortex cells (S. H. Friedman et al., 2003). There is also evidence of facilitatory interactions in the primate V1 between cells sensitive to luminance contrast and colour (Horwitz, Chichilnisky, & Albright, 2005).

It is possible that contexts, such as consistent luminance edges, are important cues to disambiguate real objects from variations in lighting. Most real objects possess clear luminance edges (Fine, MacLeod, & Boynton, 2003; Hansen & Gegenfurtner, 2009; Zhou & Mel, 2008), whereas this is not consistently the case for features less significant to awareness, such as variations in lighting (Kingdom, 2008), reflections and afterimages. It is known that perceiving a coloured surface as material rather than a light figment leads to an increase in its perceived saturation, suggesting that the visual system actively enhances the perception of objects (Bloj, Kersten, & Hurlbert, 1999). Although there are many possible means of distinguishing light from materials (see Kingdom, 2008, for a review), one possibility is that the visual system has learnt to acknowledge, or evolved to enhance, faint chromatic signals when a luminance edge is present and disregard them when it is not. This could explain why afterimages are enhanced by surrounding luminance edges.
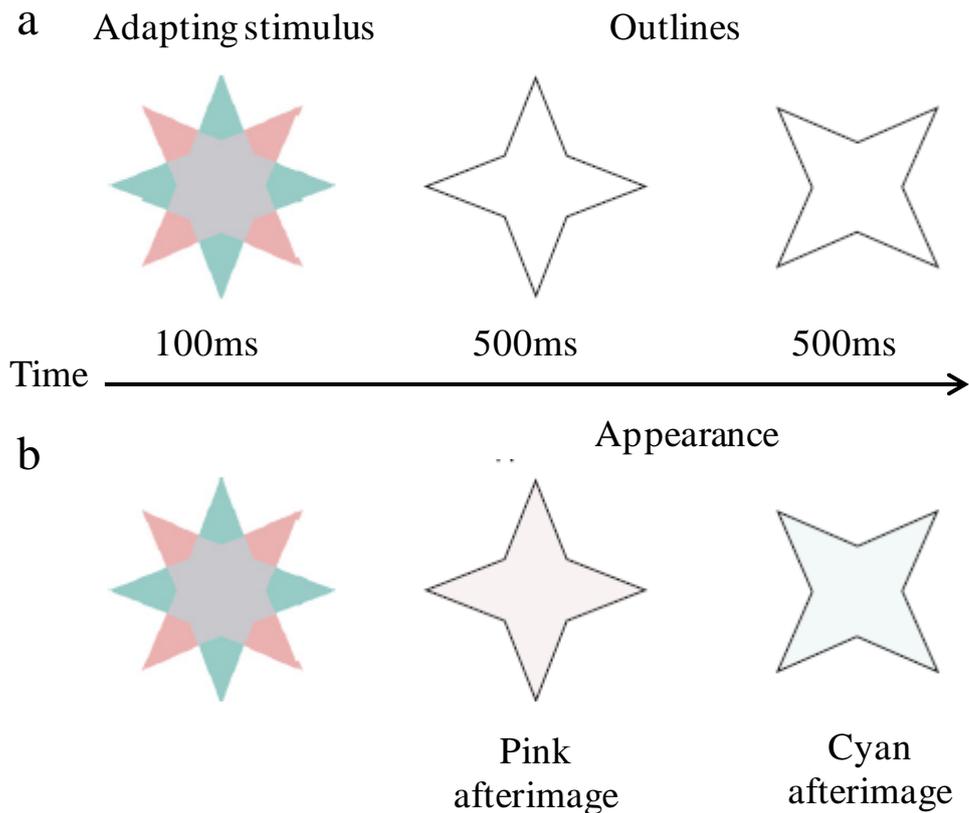
Figure 1.4. Afterimage illusion by van Lier, Vergeer, & Anstis (2009). (a) The physical stimuli continually cycle between an adapting stimulus composed of cardinal cyan triangles and oblique pink triangles (100ms), followed by two orientated outlines (500ms each). (b) The adapting stimulus produces both a pink and a cyan afterimage; however at each moment, we only perceive the afterimage that is consistent with the orientation of the currently displayed outline. Thus, a pink afterimage is seen when the outline is cardinally orientated, and a cyan afterimage is seen when the outline is oblique. The other interesting feature of this illusion is that, although only the triangles around the edge of the adapting shape are coloured (the centre is grey), the afterimages seem to fill-in to the centre of the outlines. Similar filling-in effects are found for real coloured stimuli (Mollon, 1995; Pinna et al., 2001) and these demonstrate how colour perception is very much constrained by edges. Figure adapted from van Lier, Vergeer, & Anstis (2009), p. R324.

Eye movements

 'For obtaining really beautiful positive after-images, the following additional rules should be observed. Both before and after they are developed, any movement of the eye or any sudden movement of the body must be carefully avoided, because under such circumstances they invariably vanish for a while'

-   Helmholtz (1962, p. 231)

This advice from Helmholtz illustrates the long tradition of avoiding eye movements when conducting afterimage experiments. Even though eye movements are an integral part of our everyday visual experience, they are historically absent from laboratory conditions that generate the strongest afterimage precepts. Clearly, eye movements made during an adaptation phase will dilute retinal adaptation, and thus reduce afterimage intensity. Here we are interested in whether eye movements during the test phase influence the appearance of afterimages, given equivalent adaptation.

Apart from Helmholtz, there are several other historical references to afterimages disappearing after eye movements, including those by the Darwin family (Darwin & Darwin, 1786), Holt (1903, as cited in Matin, 1974) and Fechner (1838, as cited in Wade, 1978). These observations are not without controversy - Hering (1891, as cited in Ferree, 1908) argued that afterimages are not suppressed by eye movements, particularly when viewed in the dark. It is important to note that although these authors refer to 'eye-movements', they all describe saccades. More recently, Yarbus (1967) reports saccadic eye movements performed in a darkened room produce disappearance of the afterimage if it is weak, and a change in colour of the afterimage if it is strong.

More comprehensive experiments that have explored the effect in greater detail have all reported that saccades either lead to afterimage disappearance or reduce total afterimage duration (Ferree, 1908; Fiorentini & Mazzantini, 1965; A. H. Friedman & Marchese, 1978; Kennard et al., 1970). For example, Ferree (1908) concluded that weak afterimages disappear after saccadic eye movements, while strong afterimages may still be visible during the initial eye movements directly following adaptation but their overall duration is shortened. Ferree also observed that any cue or guide that aided fixation when perceiving the afterimage increased total afterimage duration. Further, as observers' fixation improved through practice their afterimage durations increased. Friedman and Marchese (1978)

reported that the duration of afterimages generated by flashed targets (viewed in the dark) were reduced by around 50% by large amplitude saccadic eye movements.

The suppressive effect of saccades generalises to other percepts that are stabilised on the retina. Entopic images, or perceptions arising only from materials in the eye, disappear more quickly during saccadic eye movements than when the eyes remain stable (Coren & Porac, 1974; Exner, 1890). The emerging consensus is that afterimages, and other stabilised images, may disappear or change after saccadic eye movements.

The ambiguity/likelihood theory of afterimage perception

Previously we discussed that afterimages are probably generated on the retina, either through the independent adaptation of photoreceptor cells and subsequent shifts in the activity of opponent processes (Brindley, 1962; Craik, 1940; von Kries, 1970; Zaidi et al., 2012). The assumption follows that these signals are then processed by higher level visual areas equivalently to signals arising from any real stimulus. Indeed, Zaidi et al., (2012) make this explicit prediction, '..to thalamic and cortical cells, spikes transmitted as part of retinal rebound signals are no different from any other spikes from the retina' (p. 223).

However, we have noted that afterimages tend to be unstable percepts that are highly modulated by other cues, such as the surrounding context and eye movements. Interestingly, variants of the striking context-afterimage illusions we discussed earlier that display similar visibility modulation for real physical stimuli are notably absent in the literature. These observations led us to ask whether the representations of afterimages and real stimuli could actually be substantially non-equivalent in the visual brain. There may be a number of features of afterimage representations that distinguish them from responses to real stimuli, thus making afterimage signals more ambiguous. Importantly, we are not suggesting that afterimage signals and chromatic responses to real objects are not generated by the same cellular populations. Rather, that the nature of their responses – the temporal profile, the distribution of signal strengths across different brain areas, the fact they are stabilised on the retina – may not be identical in all respects (see General Discussion for elaboration). An inherent ambiguity to afterimage signals may mean that they are more susceptible to cues that increase or decrease the likelihood that they represent a real object.

The aim of Chapters 2 and 3 was to explore the ambiguity/likelihood theory of afterimage perception. In Chapter 2, we were interested in whether contextual cues (such as luminance

edges) are particularly important for afterimage visibility. Specifically, our aim was to find out whether colour afterimages are enhanced by luminance edges more than real stimuli of similar appearance. This could tell us whether the brain treats afterimages and real stimuli as 'the same', or whether there is an added uncertainty to afterimage signals that renders them more susceptible to contextual modulations. In chapter 3, we explored whether eye movements, specifically saccades, act in an opposite manner to luminance edges - by decreasing the likelihood that the afterimage represents a real object, thus leading to afterimage suppression.

Colour distortions across the visual field

So far we have discussed why afterimages might reach conscious perception under certain conditions. The second topic of this thesis is whether mechanisms exist that compensate for colour distortions across the visual field produced, in part, by the varying density of macular pigment. Macular pigment selectively absorbs short-wave light between 400 and 520nm (peak sensitivity=460nm; Bone, Landrum, & Cains, 1992), is concentrated in the central 5° and declines rapidly at greater eccentricities (Chen, Chang, & Wu, 2001). This means a higher proportion of short wavelength light reaches peripheral than foveal regions of the retina, producing a peripheral blue-green colour bias. Figure 1.5 shows macular pigment (yellow) on an image of a macaque retina, and below the perceived hue shifts for a purple stimulus between the fovea and periphery.

Retinal colour distortions are similar to afterimages insofar as they are artefacts of the retina and not meaningful properties of the world. They are also easy to demonstrate in controlled laboratory conditions but rarely infiltrate our everyday visual experience. A key difference between them is that colour variations remain fairly constant in the adult retina, while afterimages build-up and fade sporadically throughout visual experience. Given the growing emphasis on continual calibration and plasticity that we discussed earlier, it is somewhat surprising that we still perceive these colour distortions at all, especially when the evidence of an internal error remains relatively constant. Here, we first describe the pattern of colour biases across the retina and how they could be compensated, and then suggest two possible reasons why these distortions may absent from natural viewing.

Pattern of colour distortions across the visual field

There is a long standing debate about the extent to which spectral filtering differences across the visual field are translated into perceptual variations (e.g. Abramov, Gordon, & Chan, 1991; Hansen, Pracejus, & Gegenfurtner, 2009; Parry, McKeefry, & Murray, 2006; Webster, Halen, Meyers, Winkler, & Werner, 2010). Wavelengths ascribed to unique hues (i.e. those that appear pure blue, yellow, green and red) have been found to be invariant across the intermediate retina (20-50°; Beer, Wortman, Horwitz, & MacLeod, 2005; Murray, Parry, & McKeefry, 2006; Parry et al., 2006; Webster et al., 2010). However, others have suggested that unique yellow, and sometimes unique blue, are invariant, whereas unique red and green vary (Nerger, Volbrecht, & Ayde, 1995; Weale, 1953).   The prevailing consensus for intermediate hues is that purples, pinks and shorter wavelength greens shift towards blue in the periphery and longer wavelength greens and oranges shift towards yellow (Boynton, Schafer, & Neun, 1964; McKeefry, Parry, Murray, & Panorgias, 2008; Murray, Parry, McKeefry, Valberg, & Panorgias, ; Parry et al., 2006; Weitzman & Kinney, 1969).

Perceptions of achromatic stimuli are probably invariant across the retina (Beer et al., 2005; Webster et al., 2010; Webster & Leonard, 2008). Most colours also appear desaturated in the more extreme periphery (Gordon & Abramov, 1977; McKeefry, Murray, & Parry, 2007), although this is probably due to a decline in functioning of the chromatic opponent pathways at greater eccentricities (Boynton et al., 1964; Ferree & Rand, 1919; Mullen & Kingdom, 2002; Mullen, Sakurai, & Chu, 2005; Weitzman & Kinney, 1969). This decline in functioning may be due to factors such as the increasing influence of rods relative to cones (Stabell & Stabell, 1996), decreases in density of the L and M cones (Curcio et al., 1991; Parry et al., 2006), and a more random sampling of cones by ganglion cells (Abramov et al., 1991) in the periphery.
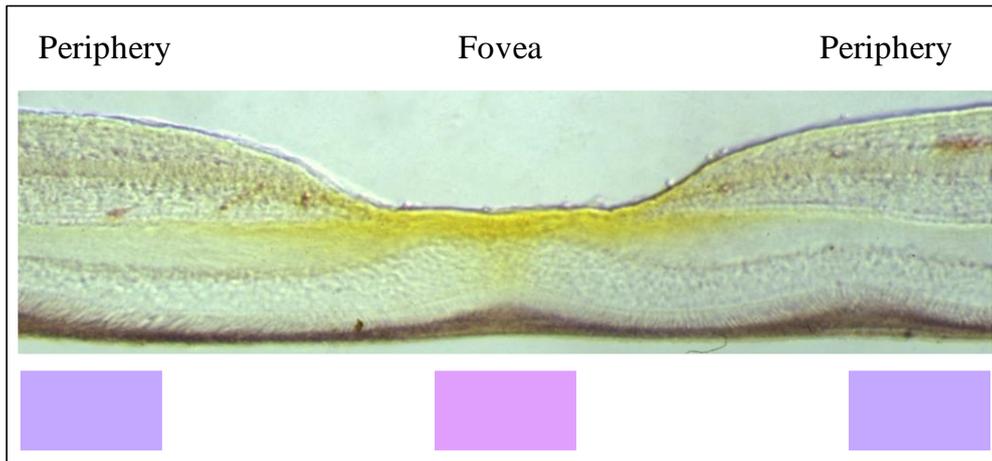
Figure 1.5. Macaque retina with macular pigment and perceptual hue shifts. A slice of a macaque retina is shown, with the fovea in the centre surrounded by two peripheral regions. Macular pigment can be seen as the yellow tinted area on the fovea. Below is the likely hue shift a purple stimulus would undergo due to macular pigment filtering of short wavelength light: a purple stimulus appears pinker in the fovea and bluer in the periphery.

Compensation for colour distortions across the visual field

An enduring task of the visual system is to ensure surface colours remain as stable as possible across space and time, a process called 'colour constancy' (Foster, 2011; Lee & Smithson, 2012). To achieve colour constancy, the visual system must compensate for both changes in the environment and also variations within the eye of the observer. There is growing evidence that the chromatic pathways that support these sophisticated processes develop through visual experience. Naturalistic light exposure from birth is critical for achieving normal colour constancy. Monkeys reared in an environment with only alternating monochromatic lights never develop normal colour constancy despite unimpaired colour discrimination (Sugita, 2004). An explanation for this is that the visual system must learn to take into account the relative activation of cones in response to the same surfaces under different illuminations but discount global changes in relative activations. Monochromatic illuminations do not allow this learning because they confine visual experience to a narrow, but constantly changing, range of relative cone activation ratios (Brenner & Cornelissen, 2005). The mechanisms that underlie this learning are probably reflective of both long-term changes in weights and connections throughout the visual system and short term adaptation through adjustments of cone gain (.e.g von Kries adaptation, von Kries, 1970; Worthey & Brill, 1986).

One way these mechanisms may be expressed is through a normalisation of the ratio of cone responses to the average stimulation, thus reducing global biases in hue appearance. Such average normalisation may underline early stages of colour constancy (Smithson & Zaidi, 2004). They may also explain why spectral filtering variations produced by age-related thickening of the yellow crystalline lens do not result in gross hue biases towards yellow in later years of life (Schefrin & Werner, 1990; Werner & Schefrin, 1993; Wuerger). Presumably, specific changes in cone gain adjust for the global yellow bias, leaving the relative cone activations to drive colour perception. It has been suggested that the gain of the S-cone pathway is adjusted for macular pigment variations, whereas the L-M pathway is not (Hibino, 1992; Stringham & Hammond, 2007; Stringham, Hammond, Wooten, & Snodderly, 2006; Werner, Bieber, & Schefrin, 2000).

These processes could explain why white remains invariant across the retina despite spatial variations in spectral filtering (Webster, 2011). However, normalisation to the average stimulation is unable to compensate for variations of non-neutral hues across the retina because spectral filtering affects different spectra to different extents. For example, the spectrum of a purple surface will produce a greater difference between the fovea and periphery than an achromatic surface because it contains high proportions of both short and long wavelength light. Thus, even after normalisation to the average stimulation, the purple surface will produce differences in LMS activation ratios between the centre and the periphery.

Sensorimotor theory of perception

The main problem for the visual system is that different relative absorptions of light between the fovea and the periphery will result in the same surface producing different activation patterns across the fovea and periphery. However, through continual sampling of the same surfaces at different locations on the retina the brain may be able to learn which ratios of activation in the centre and periphery correlate, and from this deduce that they represent the same surface colours. The sensorimotor theory of perception offers a formalisation of this process by suggesting that ongoing contingencies develop between eye movements and the visual environment (Clark & O'Regan, 2000; O'Regan & Noe, 2001). These contingencies act to promote perceptual stability, for example, by ensuring that a coin remains round when viewed with different perspectives which distort the retinal projection of the coin. Further,

these contingency laws may ensure that the same surface is perceived as similarly coloured at different retinal locations.

 In support of the sensorimotor theory, Bompas & O'Regan (2006a) found that contingencies could develop between eye movement directions and hue-changes, and these contingencies could later bias hue perception when the eyes were moving in certain directions. They adapted observers with split-hemifield coloured spectacles, so that rightward saccades were associated with a colour change from yellow to blue and leftwards saccades were associated with a colour change from blue to yellow. After removing the spectacles, rightward saccades produced a yellow aftereffect, and leftward saccades produced a blue aftereffect. Furthermore, Bompas & O'Regan (2006b) demonstrated that after successive pairings of leftward saccades to a green patch and rightward saccades to a red patch, achromatic patches on the left appear reddish and achromatic patches on the right appear greenish. On the basis of these results, it could be envisaged that similar mechanisms continuously compensate for retinal non-homogeneities and that this compensation is dependent on learnt associations between saccade direction and visual sensation.

Colour constancy across the retina is achievable but unachieved

Given that eye position and hue contingencies were developed by Bompas and O'Regan over the course of one experiment, and given that macular pigment has remained fairly stable after the age of about 2 (Bone, Landrum, Fernandez, & Tarsis, 1988), it is somewhat surprising that colour distortions across the retina are still found in laboratory settings. One possible reason for why these differences have not been extinguished through calibration is that the distortions introduced by macular pigment might not be systematic across different surfaces. For example, if light spectra were infinitely variable the visual system would not be able to generalise what it has learnt about the hue shift from one surface to predict the hue shift of another surface. In reality, natural spectra tend to be similar in shape, but the question remains over whether they are similar enough to allow for learning about the hue shifts introduced by macular pigment between the fovea and the periphery.

Data from our lab has shown that colour distortions across different commonly found objects *are* systematic enough to allow for more compensation than is actually achieved (Bompas, Powell, & Sumner, 2013). We measured the hue shifts between the fovea and periphery for 60 everyday objects and 10 standard purples from an LCD monitor and found that they were predictable enough to support compensation based on learnt hue shifts between the fovea and

periphery. We then explored how observers' perception of fovea-periphery hue differences compared to a scenario where there was no learning (i.e. only normalisation to the average simulation after chromatic viewing of a macular pigment filter) to a scenario where information based on past experience of surfaces is used to compensate for fovea-periphery differences (i.e. based on the hue shifts derived by our sample of coloured surfaces). A group of observes then completed a 3-D (hue, luminance, saturation) hue-matching staircase to obtain fovea-periphery matches for four references hues. We then compared the hue shifts obtained from this staircase to the shifts predicted from no learning (just adaptation to average stimulation) and learning (based on previous experience of coloured surfaces). We found that the degree of perceived hue biases appears to be somewhere between what is expected from basic adaptation alone and what is predicted from continuous learning. This suggests that although the visual system has partially learnt to compensate for fovea-periphery colour differences, this compensate is incomplete and less than what could be achieved given the available information.

Colour distortions under natural viewing conditions

So far we have established that colour distortions across the retina are reported in laboratory settings, and that although they are partly compensated by basic adaptation processes, compensation is not achieved to the level that should be possible given the repeatability of the exposure. The experiments in Chapter 4 aimed to confirm that colour distortions are still present in conditions that are more similar to natural viewing. We rarely perceive colour distortions in real life despite the change in macular pigment being within the spatial range of good colour discrimination. We hypothesised that a mechanism capable of complete compensation may only be activated during natural viewing conditions. We isolated two possible differences between laboratory conditions and natural viewing that could explain our failure to perceive colour variations in everyday life. First, whether colour distortions are still observed when viewing natural surfaces. Second, whether colour distortions are still perceived when the surface position remains constant but the retinal position of the surface changes due to observer eye movement.

Summary

An enduring challenge is to explain how the visual system interprets the ambiguous information it receives from early sensory detectors and forms a sensible representation of the outside world. A prolific movement in vision science aims to address this challenge through an understanding of how prior knowledge about the world is combined with new sensory information to guide the interpretation of each perceptual event, and how the machinery of the visual system calibrates to the natural world through experience. This thesis is an examination of how these processes influence the perception of phenomena that are not representative of objects in the outside world and are created solely on the retina. First, we presented an overview of afterimages and discussed how they appear to be influenced by other perceptual cues, such as context, attention and eye movements. We argued that afterimage signals may be inherently ambiguous, and thus highly susceptible to cues that increase or decrease the likelihood that they represent a real object. This hypothesis is tested in Chapter 2 (contextual luminance edges) and Chapter 3 (eye movements and blinking, and their interaction with context). Second, we discussed colour variations across the retina that are produced mainly by macular pigment filtering short wavelength light in the fovea. These colour variations are found in laboratory studies but are rarely observed in everyday life. Thus, we hypothesised that they may not be observed when viewing conditions are more natural. Chapter 4 explores this hypothesis by measuring colour variations under two 'natural' viewing conditions: with natural as opposed to computer generated surfaces, and when eye movements shift the retinal position of the surface rather than the surface itself moving.

Chapter 2: Afterimages are enhanced by contextual edges more than real stimuli

Introduction

In the General Introduction we described some compelling demonstrations of how afterimages are enhanced by consistent contexts, such as surrounding luminance edges. Physiological and perceptual research has shown that signals generated from real chromatic stimuli are also enhanced by luminance edges (Cole et al., 1990; Eskew Jr et al., 1994; S. H. Friedman et al., 2003; Gowdy et al., 1999; Hilz et al., 1974; Horwitz et al., 2005; Montag, 1997). These mechanisms may have been developed because the visual system is sensitive to the ecological frequency of meaningful objects in the world also possessing clear luminance edges (Fine et al., 2003; Hansen & Gegenfurtner, 2009; Zhou & Mel, 2008). Thus it is possible that when presented with a faint or ambiguous chromatic signal, whether it is also surrounded by a luminance edge could influence whether that signal is perceived or not.

As discussed in the General Introduction, it has long been suspected that afterimages are mainly retinal, and so many authors have assumed that subsequent processing is the same for afterimages as it is for any real stimulus of similar appearance (Zaidi et al., 2012). It follows from this assumption that afterimages and real stimuli would be enhanced equally by luminance edges. However, our hypothesis is that afterimage signals are inherently more ambiguous than signals generated from real chromatic stimuli. Thus, when presented with an afterimage signal the visual system may be faced with a dilemma over whether the afterimage should be perceived or suppressed. A surrounding context that is consistent with an ambiguous signal would raise the probability that it represents a real object, and thus raise the likelihood that it is perceived. If the signals underlying afterimages are by their nature more ambiguous than those for weak real stimuli, then we should expect that afterimage visibility will benefit more from a consistent context compared to a physical stimulus of similar appearance.

In this Chapter, we designed a series of complementary experiments to directly compare the enhancement effect of luminance edges on both colour afterimages and supra-threshold

physical stimuli. We first confirmed that luminance edges enhance discrimination of supra-threshold physical stimuli (Experiment 2.1). To explore if afterimages are enhanced by luminance edges more than real stimuli, we then used a simultaneous comparison task, in which the chromatic contrast (saturation) of a physical stimulus is adjusted to match that of an afterimage (Experiment 2.2). We also used a nulling task, in which the afterimage is nulled by a physical stimulus of complementary hue (Experiment 2.3). We then explored whether the effect of the contour on afterimages and physical stimuli was found for any surrounding edge, even if it was blurry, by substituting the contour for a sharp or blurred luminance pedestal (Experiment 2.4). Two control experiments were conducted which aimed to minimise differences between how luminance edges interact with real chromatic signals and afterimages that are not related to ambiguity (Experiments 2.5-2.6). Taken together, the experiments in this chapter produce converging evidence that sharp luminance edges (contours and pedestals) enhance afterimages to a greater extent than they do physical stimuli of similar appearance.

Experiment 2.1: Luminance contours improve discrimination of real chromatic stimuli.

We first sought to confirm previous findings that luminance contours enhance discrimination of real chromatic stimuli, specifically, of chromatic patches that had similar spatial/temporal properties to those we were to use in subsequent experiments. A method of constant stimuli was used, where pink or green patches were presented at varying saturation levels and observers were required to judge if the patches were 'pinkish' or 'greenish'. The stimuli were either framed by a luminance contour or not. Based on previous findings that luminance contrast facilitates chromatic discrimination (Cole et al., 1990; Eskew Jr et al., 1994; Gowdy et al., 1999; Hilz et al., 1974; Montag, 1997), we predicted that observers would more accurately judge the hue of increasingly desaturated stimuli when they were framed by a contour. This corresponds to an increase in the steepness of the psychometric in the contour condition relative to the no contour condition.

Pilot studies

Afterimage percepts will have blurry edges due to fixational jitter during adaptation shifting the edges of the adaptation region. Before beginning Experiment 2.1, we conducted a pilot study to calculate the appropriate amount of edge-blur to introduce to the physical patches as a precaution against a chromatic edge overshadowing any effect of the luminance contour. One observer adapted to green/pink circles (adapting circles described in detail in Methods for Experiment 2.2), for 1.5 s across 360 trials and eye movements were sampled every 4 ms. The retinal position (derived from the eye tracking data) of the stimulus at each 4 ms point during adaptation was then simulated, and these positions were translated into predicted stimulus edge blur during adaptation. This edge blur profile was then used to draw the comparison patches.

Methods

Observers

Six observers (five naive, one author; four males, two female), all with normal colour vision and normal or corrected-to-normal acuity participated.

Apparatus and Stimuli

Stimuli were presented on a 21-inch Sony GDM-F520 Trinitron monitor at 100Hz, controlled by a Cambridge Research Systems (CRS) ViSaGe and a PC running Matlab. Stimuli were viewed binocularly at a distance of 72cm, while the observer's head was maintained by a chin rest. Manual responses were made with a CRS CB6 button box. Eye movements were recorded by a CRS high speed video eye-tracker sampling at 250 Hz.

The chromaticity of the stimuli were originally calculated in MacLeod and Boynton colour space (MacLeod & Boynton, 1979), but are reported in CIE chromaticity coordinates (x,y) and luminance in cd/m^2 (Y) (Smith & Guild, 1931) for convenience. Stimuli were seven 3.5° centrally presented circular patches, consisting of four saturation levels of green (x = 0.314, y = 0.306; x = 0.311, y = 0.308; x = 0.316, y = 0.314; x = 0.313, y = 0.315; Y=28.8) and pink hues (x = 0.309, y = 0.292; x = 0.312, y = 0.299; x = 0.311, y = 0.299; x = 0.311 y = 0.3;

Y=28.8), plus one grey (x = 0.308, y = 0.316, Y = 28.8). The saturation levels were halved over successive sessions. On half the trials, the patch was surrounded by a grey 3.5° contour (x = 0.308, y = 0.316, Y =22.25). A black 0.15° fixation dot was presented in the centre of the screen to maintain fixation. All phases of the experiment were conducted on a grey background (x = 0.308, y = 0.316, Y = 28.8).

To reduce any carryover adaptation between each trial, the comparison patches were followed by a 500 ms animated mask. This consisted of pages cycling at 100Hz that each contained 200 randomly positioned and overlapping 3° circles. These circles varied either in hue or luminance. The hue range used was 10° steps around the Macleod and Boynton colour space (as represented by CRS). Circles defined by hue had the same luminance as the grey background and adapting stimuli (28.8cd/m^2). The luminance range varied from 25.8cd/m^2 to 31.8cd/m^2 in 0.3158 cd/m^2 steps. Circles defined by luminance had the same colour coordinates as the grey background (x = 0.308, y = 0.316). We did not expect the mask to influence the results because it was presented in each condition and we were interested in within subject comparisons across conditions. Also, it was presented for a very short amount of time (500ms). The risk of adaptation to some features of the mask (temporal, contrast etc) was felt to be justified in order to reduce any carry over adaptation to hue across trials.

Discrimination task

Observers viewed the patches for 700ms, and were asked to judge whether they were 'pinkish' or 'greenish'. On half the trials, the patch was framed by the contour. The patches were immediately followed by the 600ms mask. Within each session, there was a total of 14 trials types within a 2 (contour presence) x 9 (stimulus hue/saturation) within subjects design. Each trial type was repeated ten times, totalling 180 trials. The presentation of trial types was randomised. Observers completed between four to six sessions, depending on how many decrements in saturation levels were required before they reached sub-threshold performance (>75% correct) on the first saturation step.

Psychometric function fitting

Psychometric functions were obtained by fitting a logistic curve to the data using a non-linear regression procedure based on an iterative least-squares estimation technique (MatLab's nlinfit). The equation for the logistic curve is given by:

$$y = 1 / [1 + e\hat{\ }(-beta*(x-alpha))]$$

Where alpha is the centre of the psychometric function (the PSE), beta the slope, and x the data. This procedure was used throughout the thesis.

Results and Discussion

Our measure of chromatic discrimination was the steepness of the slope of the psychometric function fitted from pooled values across all sessions. A steeper slope indicates that observers can more accurately judge the stimulus hue as saturation levels decrease towards grey (see Figure 2.1a for an example psychometric function). Figure 2.1b illustrates that discrimination improved (slope consistently steeper) for all observers when a luminance contour framed the faint, edgeless chromatic patches. For two observers (4 &6) the improvement was less pronounced but in the same direction to the other observers. These results therefore accomplish the goal of Experiment 1 by confirming previous findings that chromatic discrimination is facilitated by luminance contrast (Cole et al., 1990; Eskew Jr et al., 1994; Gowdy et al., 1999; Hilz et al., 1974; Montag, 1997).
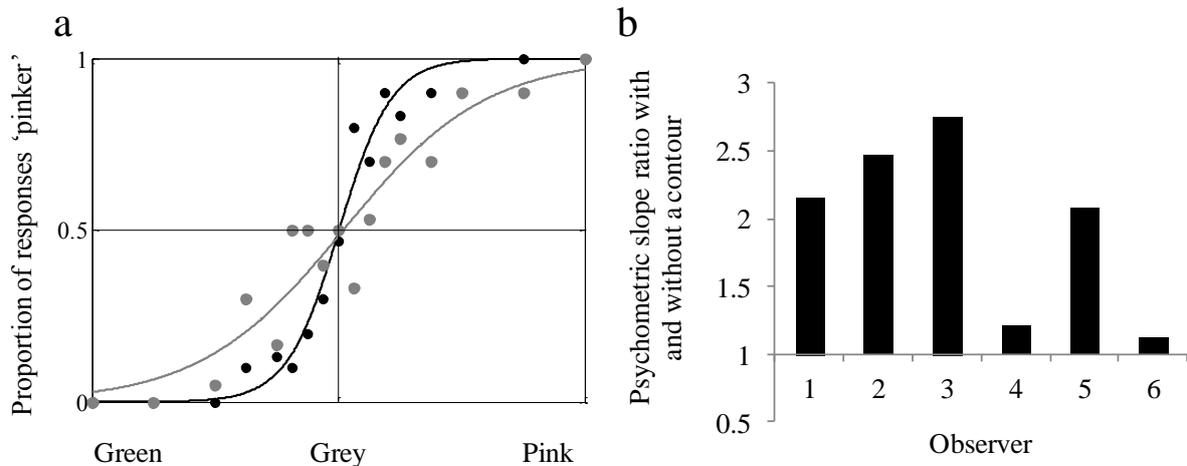
Figure 2.1. Results from Experiment 2.1 exploring luminance contour enhancement of physical chromatic discrimination. (a) Example psychometric function for the no contour (grey) and contour (black) conditions from one observer. Stimulus saturation is shown on the x-axis with steps from a highly saturated green through to grey and then to highly saturated pink, while the proportion of responses 'perceived pinker' is shown on the y-axis. The psychometric slope is steeper in the contour than the no contour condition, suggesting that this observer was more accurate at judging the hue of a stimulus at lower saturation values when the stimulus was framed by a contour. (b) Data from all six observers showing the ratio of the slope steepness in the contour and no contour conditions (contour slope/no contour slope). Four observers show an increase in slope steepness in the contour condition by an order of around 2 to 2.5. Two observers show a more moderate increase in slope steepness; these observers also had the lowest chromatic discrimination levels.

Experiments 2.2-2.4: Luminance edges enhance afterimages more than they do physical stimuli of similar appearance.

The aim of Experiments 2.2-2.4 was to test our hypothesis that afterimages would be enhanced by luminance edges more than physical stimuli of similar appearance are. We used two complementary methods of afterimage measurement: a matching task (Experiment 2.2) and a nulling paradigm (Experiment 2.3 & 2.4), and in both compared the effect of luminance edges on afterimages and real stimuli. If afterimage signals are more ambiguous than signals generated from real stimuli, we would expect an interaction whereby there is a greater increase in saturation by a luminance contours for afterimages relative to physical matching or nulling stimuli.

Observers

For Experiment 2.2, eight observers (seven naive, one author; five males, three female) participated in both the afterimage and physical stimulus comparison tasks. Four observers (three naive, one author; three males, one female) participated in Experiment 2.3 and 2.4. All had normal colour vision and normal or corrected-to-normal visual acuity.

Experiment 2.2: Afterimage and physical stimulus comparison task

Experiment 2.2 involved two stages. In the first stage, we measured the effect of luminance contours on the perceived saturation of afterimages, by asking observers to compare the saturation of afterimages, framed or not by a contour, with physical comparison stimuli that varied in saturation. In the second stage, we measured the effect of the luminance contour on the perceived saturation of a physical reference stimulus that was similar to the afterimage in hue, luminance, and contrast. In other words, we substituted a real faint stimulus in place of the afterimage and based the properties of the physical stimulus on the afterimage matching results from stage one. We conducted a pilot to ensure the physical patches were similar in appearance to the afterimages. One observer perceptually equated the hue and luminance of physical patches with the afterimage, since in the main experiments only the chromatic contrast would be modulated.

Stage 1 stimuli and procedure: Afterimage measurement

Apparatus is as described for Experiment 2.1. The adapting stimuli were green (x = 0.252, y = 0.487, Y = 28.8) or pink (x = 0.303, y = 0.171, Y = 28.8) 3° diameter circles, presented 3° to the left or right of centre. The physical comparison patches subtended approximately 3° (see explanation of edge blur below). One observer completed a pilot with a staircase to equate the hue and luminance of the comparison patches with the afterimages for a range of saturation levels (0, 10, 20, 30, 40% of the adapting stimulus saturation). The edges of the physical patches were blurred using the same profile that was used in Experiment 2.1.

Example trials are shown in Figure 2.2. All phases of the experiment were conducted on a grey background (x = 0.308, y = 0.316, Y = 28.8). During each trial of the main experiment, eight observers fixated a black 0.15° diameter central dot and were adapted for 1.5 seconds either on the left or the right of fixation. Immediately following adaptation, one of five comparison patches was presented for 700 ms on the opposite side to adaptation. On half the trials, a 3° diameter contour (x = 0.308, y = 0.316, Y = 22.25) was presented opposite the comparison stimulus (to frame the afterimage). Observers were required to respond whether the left or right patch was 'more saturated'. The comparison patches were followed by a 600 ms animated mask described in Experiment 2.1.

There were a total of 40 trial types within a 2 (adaptation hue) x 2 (contour presence) x 2 (test presentation side) x 5 (comparison patch saturation) within-subjects design. Observers received ten repetitions of each trial type, totalling 400 trials, presented in a random order. Data was collapsed across test presentation side, resulting in 20 observations at each comparison patch level for each adapting colour. Individual observer psychometric functions were fitted for each condition. From these we extracted the point of subjective equality (PSE), which represents the saturation level of the comparison patch perceived as equal to the afterimage.

Stage 2 stimuli and procedure: Physical stimulus measurement

The physical-stimuli comparison task was identical to the afterimage task, but without the adaptation phase. The physical reference stimulus was a green or pink 3° diameter circular

patch (with the same edge blur as the comparison patches) presented 3° to the left or right of centre. The saturation value of the physical reference stimulus was set to the saturation level that matched the afterimage without a contour from stage one. This was derived from the PSE between afterimage and physical stimulus in the no contour condition. These values were set individually for the green and pink afterimages and for each observer. The remaining design was the same as the afterimage stage.
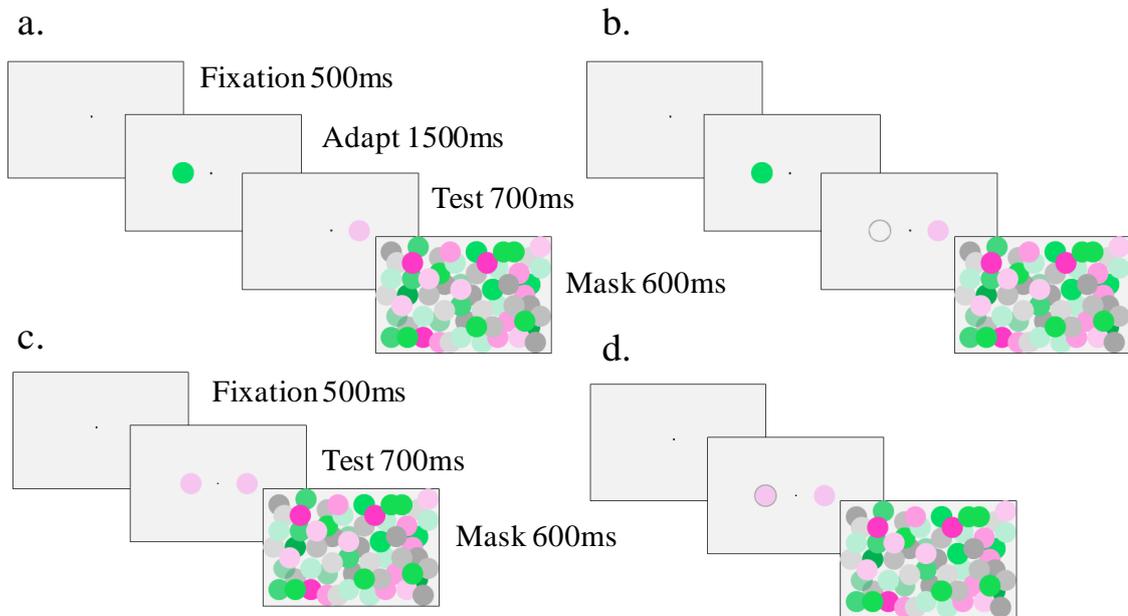
Figure 2.2. Example trials from Experiment 2.2. (*a*). *Afterimage task, no contour condition.* Observers fixate centrally and are then adapted to a pink or green circle on the left or right. One of five comparison stimuli is then presented on the opposite side to adaptation. Observers were required to indicate whether the left or right patch was 'more saturated'. Trials ended with a mask to reduce carryover adaptation. (b*). Afterimage task, contour condition.* Procedure identical but a contour is presented on the adaptation side during the test. (*c*). *Physical stimuli task, no contour condition.* Procedure identical to afterimage task but without an adaptation phase and with a physical chromatic reference stimulus in place of the afterimage. (*d*). *Physical stimuli task, contour condition.*

Experiments 2.3-2.4: Nulling task

In Experiment 2.3, we used a nulling task in which a physical stimulus of complementary hue was added to the afterimage until grey was perceived. The saturation of the physical stimulus (with and without a contour) was adjusted until the afterimage percept was nulled (the point of perceived grey, PPG). If afterimages are enhanced by luminance contours to a greater extent than physical stimuli of similar appearance, we would predict that more saturated physical stimuli are required to null the afterimages when both are framed by a contour. If the contour were to enhance both afterimage and physical nulling stimulus by the same amount, then these enhancements would cancel, and the contour would produce no shift in the PPG (only an increase in slope might be expected due to enhanced colour discrimination). We also repeated Experiment 2.3 with luminance afterimages to examine whether the effect was limited to colour afterimages.

Experiment 2.4 followed the same nulling procedure as Experiment 2.3, but employed a luminance pedestal in place of a contour. Our hypothesis was that any luminance edge would produce afterimage enhancement, whether contour or pedestal. It was important to confirm this because although the afterimage illusions that motivated our research used luminance contours, most previous reports of chromatic facilitation of physical stimuli by luminance edges have used pedestals. Further, to examine the extent to which any effect of a pedestal was due to its edge, rather than to the presence of a luminance component in the chromatic patch, we tested both sharp and blurry-edged pedestals. Previous research has suggested that facilitation of physical chromatic stimuli by luminance signals is considerably more powerful with sharp, as opposed to graded, luminance differences. For example, discrimination of chromatic gratings is enhanced by superimposed square-wave luminance to a greater extent than sine-wave luminance gratings (Gowdy et al., 1999).

Stimuli and Procedure

General apparatus and stimuli description are the same as Experiment 2.2, unless stated otherwise. In Experiment 2.3 for colour afterimages, observers fixated a central dot and were adapted for 1.5 seconds to a central 3° diameter green or pink circle. Immediately following adaption, one of the seven nulling patches was presented for 700ms. The nulling patches were

drawn with edge blur profile determined in the pilot study for Experiment 2.1 and consisted of seven saturation vectors taken from the two adaptation hues: 10%, 20% and 30% of pink and green, and one 0% (grey). The nulling patch was framed by a grey 3° diameter contour on half the trials. Observers were required to manually respond whether the patch appeared 'pinkish' or 'greenish' by pressing the appropriate response button. The nulling patches were followed by a 600 ms mask (described in Experiment 2.2). There were a total of 28 trials types within a 2 (adaption hue) x 2 (contour presence) x 7 (nulling patch hue/saturation) within-subjects design. Observers received ten repetitions of each trial type, totalling 280 trials.

For luminance afterimages, the procedure and stimulus properties were as described above was used but the colour of the stimuli were different (CIE x,y coordinates for all stimuli are the same as the background in previous studies). Observers adapted to monochromatic circles that were either dark (Y = 61.16cd/m^2) or light(Y = 13.31cd/m^2) on a monochromatic background (Y = 28.531cd/m^2). Seven luminance values were used as nulling patches which from dark to light in equal log steps through the background luminance (21.436, 23.579, 25.937, 28.531, 31.384, 34.523, and 37.975cd/m^2). The afterimages were framed by either a light (Y = 13.31cd/m^2) or dark (Y = 61.16cd/m^2) contour, or no contour. Observers were required to manually respond whether the patch appeared 'lightish' or 'darkish' by pressing the appropriate response button. There were a total of 35 trials types within a 2 (adaption hue) x 3 (light contour, dark contour, no contour) x 7 (nulling patch luminance) within-subjects design. Observers received ten repetitions of each trial type, totalling 350 trials.

For Experiment 2.4, the task, stimuli and procedure were as described for the colour afterimage part of Experiment 2.3. The single difference was that the contour was replaced by either by a sharp-edged luminance pedestal or a blurry-edged luminance pedestal that followed the blur profile used to draw the chromatic edges. There were a total of 42 trial types within a 2 (adaption hue) x 3 (pedestal type/ presence) x 7 (nulling patch hue/saturation) within-subjects design. Observers received ten repetitions of each trial type, totalling 420 trials. Example trials for Experiment 2.3-2.4 are shown in Figure 2.3.
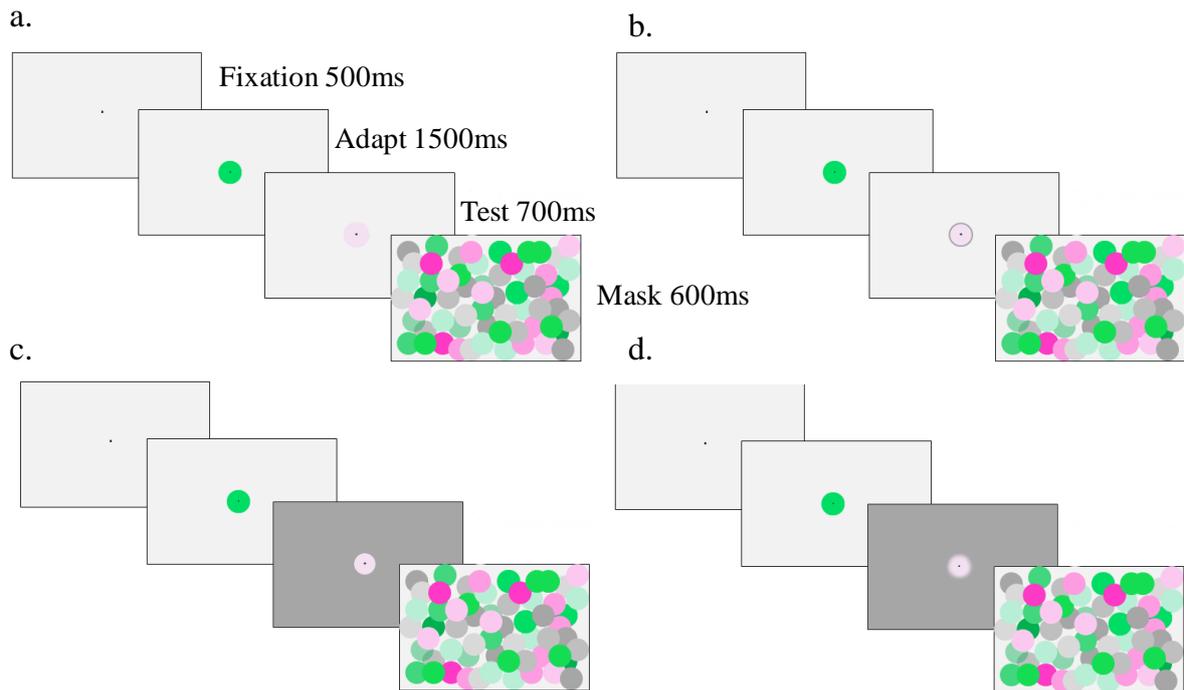
Figure 2.3. Example trials from Experiment 2.3 and 2.4. (*a*). *Experiment 2.3, no contour condition.* Observers centrally fixate and are then adapted to a green or pink circle, after which, one of seven nulling patches is presented and observers are required to respond if the circle appears 'pinkish' or 'greenish'. Trial ends with a cycling mask to reduce carryover adaptation. (*b*). *Experiment 2.3, contour condition.* Procedure is identical but the nulling patch is surrounded by a luminance contour. (*c*). *Experiment 2.4, sharp pedestal condition.* Procedure identical to Experiment 2.3, but a sharp pedestal is superimposed on the nulling patch. (*d*). *Experiment 2.4, gradient pedestal condition.* Same as above, but with a blurry pedestal.

Results and Discussion

Experiment 2.2: Afterimage and physical stimulus comparison task

Figure 2.4 shows results from Experiment 2.2 where an interaction is found between contour and stimulus type, such that the difference between the perceived saturation in the contour and no contour conditions was larger for afterimages than for physical stimuli ($F(1, 7) = 11.66$, $p < 0.01$). No main effect of stimulus colour was found and colour did not interact with the stimulus type or contour presence. These results indicate that even though the physical stimuli were similar to the afterimages in hue, luminance, degree of edge blur, and saturation, the luminance contour increased the perceived saturation of the afterimages significantly more than it increased the perceived saturation of the physical stimuli.
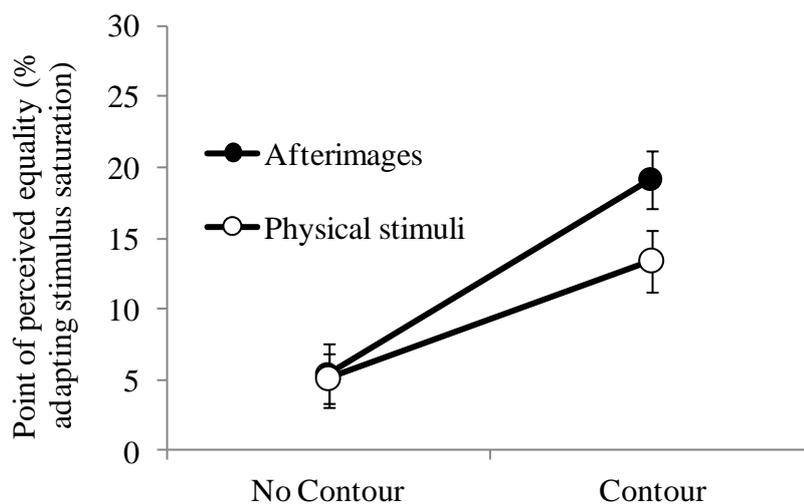
Figure 2.4. Results of Experiment 2.2. Mean point of perceived equality (units are % of adapting stimulus saturation) of afterimages (black) and real stimuli (white) in the contour and no contour conditions, across eight observers. The significant interaction is clearly shown, whereby the contour enhanced the perceived saturation of afterimages more than physical stimuli of similar appearance. Error bars show, for each condition, the standard error of the differences from each participant's mean (i.e. they are derived from the portion of the variance that is relevant for within-subject tests by excluding the irrelevant main effect of subject).

Experiments 2.3 & 2.4: Nulling task

Figure 2.5a plots the point of perceived grey (PPG) across four observers for Experiment 2.3, which represents the amount of physical stimulus saturation required to null the afterimage. For all observers, the PPG in the contour condition is shifted further away from physical grey than in the no contour condition ($t(3) = 6.51$, $p < 0.01$). This finding confirms that more physical stimulus saturation is required to null an afterimage that is framed by a contour. We found no consistent increase in the slope of the PMF in the contour condition, providing no evidence that the contour improves discrimination of the combined stimulus (the afterimage and the null).

The contour effect on afterimages is not specific to chromatic afterimages; Figure 2.5b shows the results of a luminance afterimage nulling experiment where observers adapted to light, monochromatic patches and the resultant afterimages were framed by a light contour, dark contour or no contour. As shown in Figure 2.5b, both light and dark contours tended to shift the PPG relative to the no contour condition, indicating that the afterimage enhancement exceeded that for the physical nulling patches.

Figure 2.5c shows results from Experiment 2.4, in which sharp and blurred pedestals were presented instead of a contour. The mean shift in PPG across observers is greater in the sharp pedestal condition compared to the no pedestal and blurry pedestal conditions ($F(2, 6) = 8.88$, $p < 0.05$). Post hoc tests revealed that the perceived saturation of the afterimages in the sharp pedestal condition was significantly greater than both the blurry pedestal and no pedestal conditions ($p = 0.041$ and $p = 0.023$ respectively). In contrast, the blurry pedestal condition was not different to the no pedestal condition ($p = 0.554$). This suggests that the benefit in the sharp pedestal condition depends on the presence of a sharp edge, rather than the mere presence of a luminance increase congruent with the colour gradient. For all but one observer the psychometric slope in the sharp pedestal condition was steeper that the no pedestal or blurry conditions. This suggests that the discrimination of the combined stimulus (the nulling stimulus and the afterimage) was improved by a superimposed sharp pedestal, a finding consistent with previous findings for the enhancement of real chromatic stimuli. Further, the importance of edges for chromatic perception is demonstrated in examples of chromatic spreading and 'filling-in', such as the Boynton and watercolour illusions (Mollon, 1995;

Pinna et al., 2001). Why we observed improved discrimination in the sharp pedestal condition here, but not with the luminance contours in Experiment 2.3, is unknown.

Taken together, the results of Experiments 2.2-2.4, suggest that the contextual modulators of afterimage visibility seen in recent compelling afterimage illusions (Sadowski, undated; van Lier et al., 2009) is not observed to the same degree for real, faint chromatic stimuli. Thus, although previous research has demonstrated that real chromatic stimuli are enhanced by luminance edges, our findings indicate that afterimages are enhanced by luminance edges more than physical patches. This finding implies that there may be something different about afterimage representations that results in particularly powerful modulations by contextual cues (in this case, luminance contours).

a. **Experiment 2.3 – colour afterimages**

b. **Experiment 2.3 – luminance afterimages**

c. **Experiment 2.4 – pedestals**
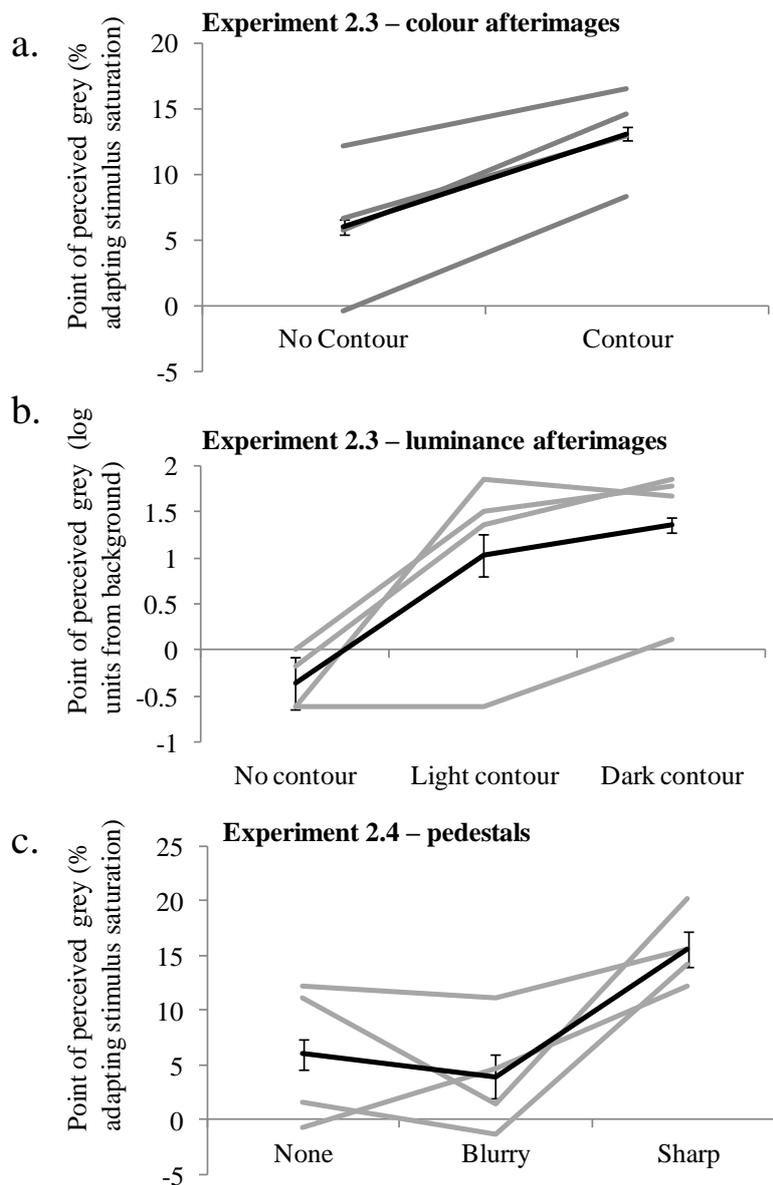
 Figure 2.5. Results from Experiments 2.3-2.4. Grey lines represent individual observers, black is the mean across observers. Error bars calculation is the same as described for Experiment 2.2. There are 20 data readings for each individual observer point. *(a). Experiment 2.3.* Point of perceived grey (in % of adapting stimulus saturation) in the no contour and contour conditions. Across all observers, more physical saturation is required to null the afterimage in the contour condition compared to the no contour conditon. (*b). Nulling procedure replicated with lumianance afterimages.* Individual data from four observers in the no contour, light contour and dark contour conditons. The point of perceived grey (PPG), or the point at which nulling patch is judged perceptually equal in luminance to background, is plotted in log units from the background. Dark contours consistently shifted the null point compared to the no contour condition. Light contours shifted the PPG in a similar direction for three out of four observers. (*c).* Mean physical saturation required to null the afterimage (PPG, units are % of adapting stimulus saturation) across sharp, blurry and no pedestal conditions, across four observers. Figure illustrates that a sharp pedestal increases the perceived saturation of the afterimage compared to the no pedestal condition. Whereas, a blurry pedestal does not increase the saturation of afterimage above the no pedestal condition.

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Control experiments (2.5-2.6)

We conducted two further experiments to control for other differences between the afterimages and physical stimuli that could have driven the different degrees of contour enhancement found in Experiments 1-3.

Control 1 (Experiment 2.5): Were the edges of the physical stimuli blurry enough?

The larger contour effect for afterimages compared to real stimuli could be due to an underestimation of afterimage edge blur. If the edges of the physical stimuli are less blurry than those of the afterimages, we might expect to find less modulation by the contour, because sharper chromatic edges may themselves contribute to the contour/edge effect. The edge blur profile used to draw the physical patches was based on eye movement jitter from one observer, and analysis of the jitter from other observers revealed some variance with this standard (Experiment 2.2: three lower, five higher than standard; Experiment 2.3: three higher, one lower than standard). Although no correlation was apparent between this jitter and the difference between the afterimage and physical stimulus contour effects, these correlational analyses had very low power. Therefore we tested the effect of edge blur in a further comparison experiment, identical to the physical stimulus conditions described for Experiment 2.2.

The edge blur of the reference stimulus was modulated from increased blur to sharp edged and presented with and without a luminance contour. There were three levels of edge blur: sharp edge stimuli, standard blur (blur from Experiment 2.1-2.4), increased blur (produced by adding Gaussian noise with 5 mm SD to the blur used in Experiment 2.1-2.4. See Figure 2.6). There were two physical reference stimuli, one green ($x = 0.311$, $y = 0.316$; $Y = 28.8$) and one pink ($x = 0.308$, $y = 0.278$; $Y = 28.8$). Saturation of the physical reference was measured using a comparison paradigm similar to Experiment 2.2. The saturation of the comparison patches was set to 0, 100, 150, 200 and 250 % of the physical reference saturation.

Experiment 2.5a used a fixed saturation level of the physical reference across blurriness conditions, whereas in Experiment 2.5b the saturation of the physical reference was adjusted to achieve perceptual equivalence across blurriness conditions (to ensure that differences in perceived saturation across blurriness conditions did not mask differences in contour modulation). Six and three observers participated in Experiments 2.5a and 2.5b respectively.

There were a total of 160 trials types within a 2 (stimulus hue) x 2 (contour presence) x 2 (stimulus presentation side) x 5 (contour onset) x 5 (nulling patch saturation) within-subjects design. Observers received five repetitions of each trial type, totalling 800 trials. Results were collapsed across stimulus presentation side. The trial type presentation was randomised and the experiment was conducted over 6 sessions to minimise observer fatigue.
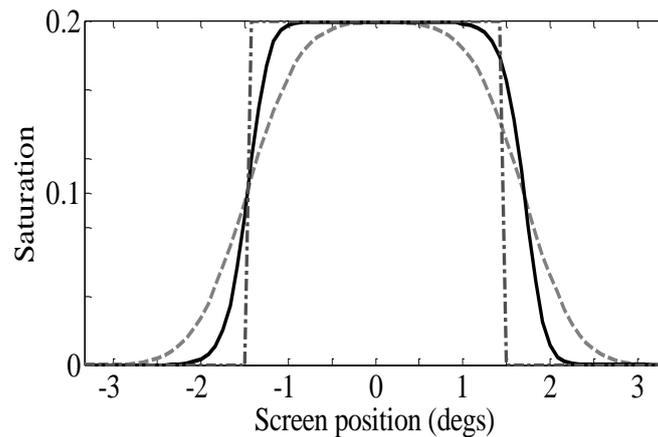
Figure 2.6. Screen profiles of saturation levels for edge blur conditions in Experiment 2.5: sharp edge standard blur (black), sharp edge (dark grey), increased blur (light grey).

The results showed that the contour effect did not increase as the edges of the patches became increasingly blurry (Figure 2.7). Specifically, there was no interaction between the contour effect and degree of blur when the reference stimuli were physically equally saturated across edge blur conditions (Figure 2.7a). This was also the case when the perceived saturation levels of the reference were equated across levels of edge blur (Figure 2.7b).

Perceived saturation was equated to counteract changes in saturation due solely to edge blur, as we wanted to be sure that this did not interact with the contour effect. These findings indicate that even if the blurriness of our physical stimuli was underestimated for some observers in Experiments 2.2-2.4, this is unlikely to explain why we found increased contour modulation of the afterimages relative to physical stimuli, because increasing edge blur does not lead to an associated increase in contour modulation.
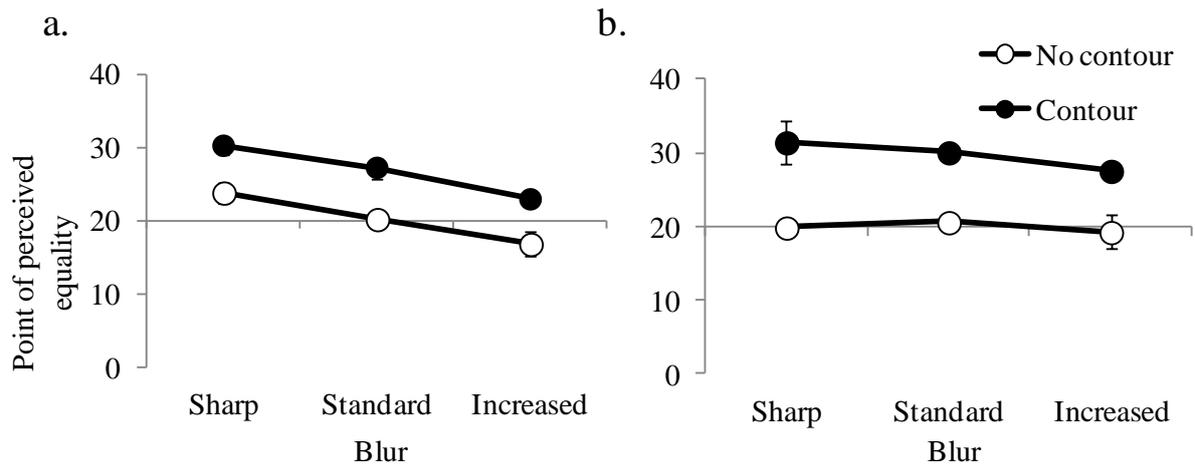
Figure 2.7. Results of Experiment 2.5. Perceived saturation of the reference from the physical saturation, across edge blur and contour conditions, when the patches were equally physically saturated *(a)* and when they were perceptually equally saturated *(b)*. Physical saturation for the reference was 20. Both illustrate that, although the contour increases the perceived saturation of the reference, it does not do so in a way that interacts with the blurriness of the reference. Error bars calculated in the same manner as Experiment 2.2 (some are smaller than the marker size).

Control 2 (Experiment 2.6): Temporal order of contour and physical stimulus onsets.

Another possible explanation for why afterimages were enhanced to a greater extent by edges compared to the physical stimuli is that adaptation signals are present in the visual system prior to the presentation of the contour or the physical stimuli. Indeed, as luminance signals tend to reach the visual cortex 10-30 ms before chromatic signals (Bompas & Sumner, 2008; Maunsell & Gibson, 1992; Nowak, Munk, Girard, & Bullier, 1995; Schmolesky et al., 1998) and the adapted colour signal is present before this, the afterimage will benefit from any contour enhancement prior to the physical stimulus.

In order to control for this difference, three observers repeated the afterimage and physical stimulus comparison task (Experiment 2.2). However, we varied the onset of the contour so that it was presented either 0, 20, 40, or 60 ms after adaptation or physical stimulus onset. If the physical stimulus suffered from arriving in the cortex after the contour, we might predict its contour effect to increase for a contour delay of 20-40 ms. Contrary to that prediction, results revealed the contour effect remained fairly stable between contour onsets of 0-60 ms for both afterimages and physical stimuli, suggesting that contour onset does not notably

modulate contour enhancement effects (Figure 2.8). Further, the contour effect was greater for afterimages than physical stimuli, thus replicating the results of Experiment 2.2.
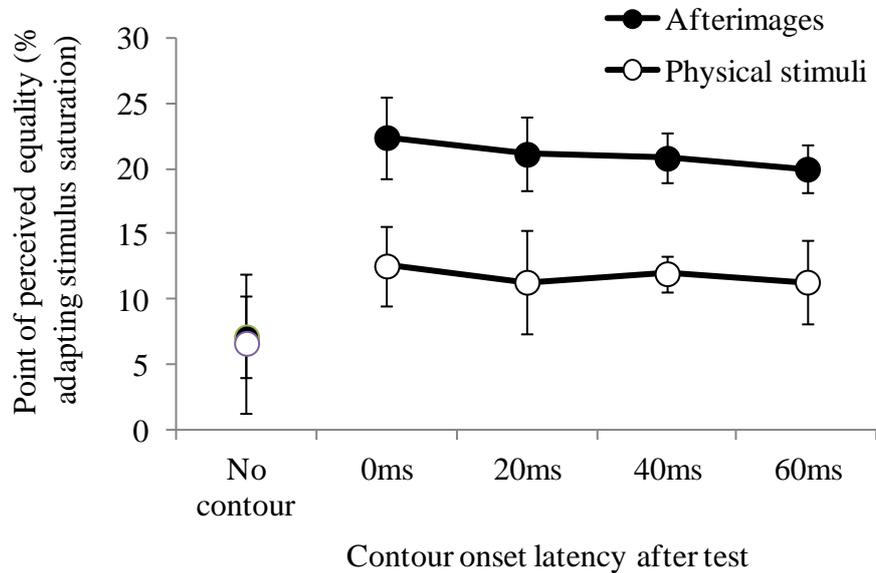
Figure 2.8. Results of Experiment 2.6. Perceived saturation of afterimages (black) and physical stimuli (white), with and without a contour, across four contour onset times. The no contour and 0 ms onset points are a replication of Experiment 2.2, and show that both afterimages and physical stimuli were perceived as equally saturated when not framed by a contour (as expected from the experimental design), but afterimages were perceived as more saturated when framed by a contour than were physical stimuli. However, the pattern is similar across different contour latencies showing that contour onset time did not interact with the contour effect or the type of stimulus (physical or afterimage). Error bars calculated in the same manner as Experiment 2.2.

Chapter 2 Discussion

We investigated whether negative colour afterimages are treated identically to real, physical stimuli. We proposed that there are differences between the adaptation response that results in afterimage percepts and signals from physical stimuli, and that these differences may lead to a different degree of luminance edge modulation of afterimages compared to real stimuli. Our theory was motivated by noting the absence of physical stimulus versions of illusions demonstrating compelling contextual modulations of afterimage visibility.

Afterimages are particularly enhanced by context

We first confirmed that luminance edges enhanced discrimination of real chromatic stimuli (Experiment 2.1). We then reported converging evidence from both a comparison and nulling paradigm that luminance edges (contours or pedestals) enhanced the visibility of colour afterimages to a greater extent than they did for physical stimuli of similar appearance. In the comparison experiment (Experiment 2.2) the physical stimuli were similar to the afterimages in appearance (hue, luminance and saturation), yet were not enhanced by the contour to the same degree. The nulling paradigm (Experiments 2.3 and 2.4) revealed that more physical stimulus saturation was required to null the afterimages when framed by a luminance edge. This result excludes the possibility that the edge enhanced both the afterimage and the physical nulling patch equally, which could have resulted in an overall increase in discrimination when the contour was present, but not the observed shift in the null point. This is because the contour would enhance discrimination of the combined signal of the nulling patch and the afterimage. Our findings are not constrained to chromatic stimuli, because we replicated the results of Experiment 2.3 using luminance afterimages.

A control study (Experiment 2.5) revealed that the difference in contour enhancement between afterimages in physical stimuli was not due to an underestimation of the edge blur used to draw the physical patches (fixational jitter during adaptation will blur afterimage edges). We found that increasing or decreasing the blurriness of the physical patches did not lead to a decrease or increase in the size of the contour effect. A further control study (Experiment 2.6) revealed that our results do not arise from temporal differences in the onset of afterimage versus real signals. Contour enhancement was greater for the afterimages compared to physical stimuli, thus replicating the results of Experiment 2.3. However,

delaying presentation of the contour a (0-60 ms) after presentation of the physical stimulus did not impact the degree of contour modulation.

Afterimages as ambiguous stimuli

Our finding that luminance edges enhance afterimages to a greater extent than they enhance physical stimuli suggests that afterimage representations are processed to some extent differently to signals arising from real world objects. One possible reason for this effect is that afterimages are ambiguous, like other phenomena such as binocular rivalry and ambiguous figures. For example, the tendency of afterimages to fade in and out of conscious awareness (Wade, 1978), especially when not supported by a consistent context, could be analogous to the perceptual oscillations present during binocular rivalry. Increased ambiguity, whatever its source, is likely to result in greater susceptibility to contextual modulation. Moreover, in everyday viewing, such context would be powerful enough to suppress the perception of afterimages most of the time. Support for these suppression effects is found in the experiments of Daw (1962) and in the illusion by van Lier, Vergeer, & Anstis (2009), where afterimage percepts are inhibited when the context is inconsistent with the afterimage (see also our 'Welsh Castell Coch' demo in the Appendix where the afterimage is suppressed when the context is presented upside down). This might explain why we do not often perceive afterimages in everyday life despite the ease with which they can be evoked in demonstrations and illusions.

Although we are not arguing that the underlying cellular populations differ between afterimages and perceptions of real chromatic objects, there are a number of plausible reasons (which we will discuss in the General Discussion) for why the pattern of activity in these cells may be importantly different between afterimages and real stimuli. If the perceptual system is attuned to these differences, the afterimage signals will present uncertainty – in some ways the signal will be like that of a real stimulus, but in some ways it will not be. In this situation, perception will be particularly influenced by any disambiguating cues, such as luminance edges, that increase the likelihood of the signal representing a real object.

At a general level, our explanation relies on the assumption that it is beneficial for perception to dissociate afterimage signals from signals arising from real world objects. Previous studies

have shown that a coloured surface is perceptually enhanced if it is interpreted as material (i.e an object) rather than an illumination (Bloj, et al., 1999; Kingdom, 2008). Afterimages could be considered similar to signals arising from illumination, but may even possess added ambiguity. That is, the visual system may have prior knowledge (implicitly, in the pattern and weights of its connections) of the typical activation profile associated with responses to real world objects. If signals arising from adapted cells deviate in any way from the typical profile associated with real objects, this could lead to the interpretation that the afterimage signal is illusory. Thus perception of the afterimage is suppressed.

More specifically, we assume that luminance edges and other contextual cues support the interpretation that an ambiguous signal represents a real object. This interpretation may have been learnt based on real world statistics that most objects are delineated by luminance and chromatic contrast (Fine et al., 2003; Hansen & Gegenfurtner, 2009; Zhou & Mel, 2008), whereas this is not as likely for features less significant to awareness (e.g. illuminations, reflections).

How context could modulate chromatic signals

Perceptual demonstrations of filling-in and psychophysical research both demonstrate that luminance edges are important for constraining and facilitating chromatic signals (Chaparro et al., 1994; Cole et al., 1990; Eskew Jr et al., 1994; Gur & Akri, 1992; Hilz & Cavonius, 1970; Hilz et al., 1974; Montag, 1997; Mullen & Losada, 1994). In our experiment, a sharp edge was critical for enhancement above the mere presence of a luminance difference, as we observed that blurry-edged pedestal did not enhance the afterimage as much as a sharp contour or pedestal. A luminance sine-wave grating does lower chromatic threshold, though not to the extent of square-wave gratings (Gowdy et al., 1999). That the edge closely frames the chromatic signal is also important, as orthogonal edges do not produce the facilitation observed with contiguous edges (Gowdy et al., 1999). Higher-level edge representations, such as stereoscopic-depth edges and illusory contours also modulate chromatic representations (Montag, 1997). This suggests that as long as the edge makes sense in terms of a higher level context it produces facilitation. It also seems important for facilitation that the edges are supra-threshold (Chaparro et al., 1994).

The fact that chromatic facilitation is reliant on sharp edges, even if the properties of these edges are somewhat abstract, suggests that it is mainly a cortical process rather than just a low-level luminance interaction. This is in line with physiological research that orientation and form become increasingly important at higher levels of the visual system (S. H. Friedman et al., 2003). Further, they may begin to influence other features such as colour. For example, responses of blue-yellow colour-opponent neurons in the macaque V1 are facilitated by luminance contrast (Horwitz et al., 2005).

Relation to associative learning and McCullough after-effects

One possible explanation for the contour effects observed in these experiments is that the sharp edge of the adapting stimulus was associated with the perception of a coloured hue, and the contour triggered this association thus leading to a heightened perception of the coloured afterimage. This association would be formed within the experiment, rather than reflecting long term association between coloured objects and luminance edges that were described previously. Associations between orientation and colour have been used to explain long-lasting colour afterimage effects, such as the McCullough effects (described in the General Introduction). However, it is unlikely that a short term associative learning account can explain the present findings for a number of reasons. First, the contour effect is evident immediately on the first trial and does not appear to change in intensity over time. Although it is possible to form an association after only one presentation, the stimuli must be extremely salient. The McCullough effects, which in essence depend on the same type and intensity of stimuli – hue and luminance lines – require a very long adaptation exposure to develop. Second, the association work best when the associated stimulus is similar to the stimulus used to evoke the association. In the case of our experiments, the adapting stimulus edge and its centre are both very dissimilar to the contour and the complementary afterimage, in terms of hue, luminance and spatial structure. For example, weak associative strength would be expected between a homogenous pink edge with a homogenous pink centre and a grey contour and a green centre. Third, pilot experiments we have conducted suggest that the contour effect is present even when the adapting stimulus has blurry edges, thus removing the sharp edge association.

Summary

In this Chapter, we presented converging evidence that luminance edges enhance afterimages more than they do physical stimuli of similar appearance. This finding appears to be specific to sharp edges, as a graded luminance pedestal did not produce the afterimage enhancement found with a sharp pedestal or contour. These results demonstrate that the brain processes signals arising from adapted cells non-equivalently to those arising from real stimuli. We suggest that because signals that generate afterimages percepts fail to perfectly match those arising from real stimuli, the visual system is unsure of whether the afterimage represents the presence of a real object or not. This would explain why afterimages are influenced by contextual cues that reduce their uncertainty more than responses triggered by real objects. Conversely, in everyday viewing contextual cues will be unlikely to align with afterimages, and thus our perception of them is often suppressed.

Chapter 3: Eye-movements, blinking, contextual edges and afterimages

Introduction

Chapter 2 established that luminance edges are powerful modulators of afterimage visibility and they appear to enhance afterimages more than real stimuli of similar appearance. We suggest that this is perhaps because afterimage signals are fundamentally more ambiguous. In this chapter we were interested in cues that could act in an opposite manner to luminance edges and decrease afterimage perception. In the General Introduction, we reviewed evidence dating back to the early 18th century that saccadic eye movements reduce afterimage duration or cause them to disappear immediately (Coren & Porac, 1974; Darwin & Darwin, 1786; Ferree, 1908; Fiorentini & Mazzantini, 1965; A. H. Friedman & Marchese, 1978; Helmholtz, 1962; Kennard et al., 1970; Yarbus, 1967). These effects are also found for other stabilised images (Coren & Porac, 1974).   The experiments in Chapter 3 aimed to explore why saccadic eye movements might influence afterimage perception and also investigate how eye movements and luminance edge cues are combined in their modulation of afterimages.

Why do eye movements influence afterimage perception?

Just as there is a long, if sporadic, literature reporting that saccades diminish afterimage perception, there is a similar history of suggested explanations for the effect. This is not an area where there has been consistent cross-talk between theorists, but it is possible to classify them into four main categories, the first and fourth of which are directly related to ideas developed in Chapter 2. First, it is possible that saccades simply misalign afterimages with the background context (e.g. luminance edges), thus leading to a reduction in afterimage perception for the reasons explored in Chapter 2.   Similarly, other visual interactions could occur during saccades that could interfere with afterimage perception, such as luminance changes and smearing of the visual field. Second, saccades could disrupt the physiological state of the retina in a way that relieves adaptation. Third, thresholds for perceiving real stimuli are reduced by saccadic suppression mechanisms, thus afterimage suppression could occur through similar processes. Fourth, saccades could distinguish an afterimage from a real

object because they decorrelate signals that are stationary on the retina from signals that are stationary in the world. We now discuss the evidence for these theories in greater detail.

1. Changes to the retinal image

In Chapter 2 we argued that background context can greatly influence afterimage perception. In our experiments we showed that perceived afterimage saturation is increased when the afterimage is framed by a luminance edge. Afterimages can also be suppressed when presented on a background context that is inconsistent with the afterimage (Daw, 1962). In illuminated, structured environments, it is unlikely that when the eyes move the afterimage will align perfectly with the contours of the background. Thus, we would expect that our perception of the afterimages would be reduced by saccades. However, most of the experiments that have explored the effect of saccades on afterimage perception have been conducted either on uniform backgrounds, or more commonly, in the dark. Under these conditions, the change in context is minimal. Thus, although context is an important modulator of afterimage perception, it cannot explain the findings that saccades reduce afterimage perception in conditions where there can be no change in the alignment of the afterimage and the background edges.

Although saccades on uniform backgrounds may not produce changes in higher level contexts, they could still produce lower level, less specific, changes at the retina. This idea was adopted by many early theorists, although exactly what these changes are has been the subject of some debate. Helmholtz (1962) argued that eye movements produce illumination changes on the retina and this leads to afterimage disappearance. More recently, it has been shown that intermittent luminance modulation of the background can actually prolong afterimage duration (Gerling & Spillmann, 1987; Magnussen & Torjussen, 1974; Matteson, 1965; Robertson & Fry, 1937). All of these experiments studied afterimages that were probably a consequence of photo pigment bleaching, because they were generated by intense light flashes. It remains possible that changes in luminance could affect ganglion afterimages differently to photochemical afterimages.

Hering (1891, as cited in Ferree, 1908) believed that any previous finding showing that afterimages disappeared after an eye movement was due to secondary changes on the retina produced by the saccade, rather than a unique saccade mechanism. In support of his

argument, Hering noted that similar effects can be found by rapidly shifting the background to simulate retinal changes such as smearing. Hering also argued that afterimages do not tend to disappear after saccades in the dark when no retinal change occurs.

However, Hering based his arguments on the observation that an afterimage of an intense stimulus will not disappear after one eye movement, thus overlooking the effect of saccades on weak afterimages and the shortening of their total duration after continual eye movements. Furthermore, Ferree claims that moving the background (composed of a grey mottled sheet of cardboard) does not produce afterimage disappearance when it is ensured that the eyes do not also move with the background. From his own observations, Ferree also reported that afterimages do disappear when saccades are made in various dark conditions (eye closed and covered in black cloth, in a dark room with eyes open and closed, and in a blackness cylinder). These findings are supported by numerous later authors who have reported that saccades reduce afterimage perception when viewed in the dark (Fiorentini & Mazzantini, 1965; A. H. Friedman & Marchese, 1978; Kennard et al., 1970). Thus, although it is possible that changes to the retinal image produced by eye movements could influence perception, these theories struggle to explain the influence of saccades on afterimages viewed in the dark and on uniform backgrounds.

2. *Physiological changes associated with eye muscle movement*

Other early theorists focused on the physiological effects produced by the movement of the muscles themselves, rather than the changes to the retinal image. The advantage of these theories is that the related processes would still operate in dark conditions. Fechner (1838, as cited in Wade, 1978) suggested that eye movements cause disturbances to vascular and nervous mechanisms on the retina, for example, by producing temporary vascular congestion. These mechanisms then disrupt the adaptation state on the retina. Similarly, Flick and Gurber (1889, cited by Exner, 1890; Matin, 1974) suggested that eye movements stimulate the 'lymph stream' with new signals produced by eye muscle movement, and this enables the retina to recover. However, it is unclear what the 'lymph stream' relates to in our modern understanding of retinal physiology, immediately creating a barrier to assessing how viable Flick and Gurber's theory is. A similar argument can be applied to Fechner's theory of vascular congestion. Movement of the extraocular muscles does produce a slight increase in intraocular pressure (IOP, Murgatroyd & Bembridge, 2008). High IOP is associated with less blood flow to the retina. However, these effects are unlikely to occur with a relatively small

increase in IOP produced by saccades because blood flow to the retina is autoregulated to adjust for changes in IOP (Flynn, 2003; Kaufman, Alm, & Adler, 2003). Apart from this, we have not identified any eye movement mechanisms that could produce changes to the vascular state of the retina.

However, even if these physiological changes do occur and can influence the state of adaptation, they cannot explain why entopic images, where no recovery from fatigue is required, are also suppressed by eye movements (Exner, 1890). Furthermore, it is not obvious how disruption to the adaptation state on the retina by eye movements can explain why afterimages disappear briefly after a saccade and then reappear (Ferree, 1908; Fiorentini & Mazzantini, 1965; Kennard et al., 1970).

3. Saccadic suppression or masking

Since the above theories were developed, we now know a great deal more about how real stimuli are suppressed during saccadic eye movements. Thresholds for perceiving a stimulus, such as a flash of light, are raised when it is presented briefly before, during, or after a saccade – an effect known as saccadic suppression, masking or omission (Volkmann, 1962). Recent explanations for this effect suggest that efferent signals about an impending saccade suppress visual responses from the retina before and during the saccade, and then backward masking from re-fixation point signals prevents these suppressed signals from reaching conscious perception (Ibbotson & Cloherty, 2009). It is probable that Yarbus (1967) was attributing the disappearance of afterimages to saccadic suppression when he discussed a partial inhibition of perception during a saccade resulting in afterimage disappearance. Saccadic suppression could explain why afterimages are completely suppressed during continual, fast saccadic eye movements but return during periods of fixation when the saccade frequency is slower (Kennard et al., 1970). Rapid saccades could trap the perception of the afterimage within a continual state of saccadic suppression. Unlike contextual theories, saccadic suppression could explain why afterimages are still suppressed in the dark and on uniform backgrounds.

If saccadic suppression is wholly responsible for the effect of saccades on afterimages, we would expect that the parameters that influence saccadic suppression of afterimages and real stimuli to be similar. There is some evidence in support of this; saccadic suppression of real

stimuli increases with the magnitude of the saccade (Ridder III & Tomlinson, 1997) and some researchers have found that afterimages will be suppressed for longer after larger amplitude saccades (Kennard et al., 1970).

However, others have reported that saccade amplitude is not associated with the time it takes for an afterimage to reappear (Fiorentini & Mazzantini, 1965).   In any case, afterimage suppression is much longer-lasting than the transient decrease in sensitivity for real stimuli slightly before and after a saccade (Ferree, 1908; Fiorentini & Mazzantini, 1965; Yarbus, 1967). Further, Richards (1968, as cited by Matin, 1974) found that the perception of a brief flash presented on a background that is composed of an afterimage improved when a saccade was performed just before the flash. The explanation given for this result is that the saccade reduces the noise introduced by the afterimage signals on the background and thus facilitates perception of the real light flash. This implies that the mechanisms underlying saccadic suppression of afterimages and real stimuli may be different. Indeed, we suggest that the much longer time course of suppression that afterimages undergo after a saccade and the decrease in afterimage duration means that saccadic effects on afterimages must be different, or at least involve additional mechanisms, to classic suppression effects observed for real stimuli.

4. Saccades distinguish an afterimage from a real object.

In Chapter 2, we argued that luminance contours are important cues that modulate afterimage visibility because they increase the likelihood that the afterimage represents a real object. It is possible to view saccades as another cue that modulates whether the afterimage signal is interpreted as a real object or not. Fiorentini and Mazzantini (1965) discussed the possibility that the "lack of any retinal change during an (eye) movement provides evidence against the presence of a real stimulus" (p. 319). This is reminiscent of a theory by Exner (1890), who distinguished 'subjective phenomena'- or perceptions arising only from the eye (afterimages, entopic images) - from 'objective phenomena' -or perceptions of real world objects. Exner (1890) argued that eye movements could differentiate a subjective percept from an objective one because objective phenomena do not move with the eyes, while subjective phenomena always do because they are fixed on the retina. Put another way, it is not possible for the visual system to distinguish an afterimage from a real object when the eyes are fixated,

however, as soon as the eyes move the afterimage behaves in a way that is unlike any real object. This cue that the afterimage is 'subjective' leads to its suppression.

If Exner's (1890) terminology is updated so that objective and subjective are expressions of the likelihood a signal represents a real object, his ideas mirror the hypothesis formulated throughout this thesis: saccadic eye movements provide another cue to distinguish an afterimage from a real object. While a consistent context increases the likelihood that the afterimage represents a real object, a saccadic eye movement may decrease this likelihood.

Exner's theory is supported by findings that entopic images of Haidinger's brushes fade faster when observers make saccadic eye movements than when they fixate (Coren & Porac, 1974). Although Coren and Porac (1974) do not reference Exner, their explanation of their findings is very similar: entopic images fade faster during saccades because the retinal image no longer correlates with the eye movement signal, and this decorrelation results in a cessation of perceptual responding to the stabilised image.

This theory allows us to make predictions about how other types of eye movements will influence afterimage perception. For example, if saccades suppress afterimages because they increase the likelihood that the afterimage is illusory, we may not expect to find that pursuit eye movements suppress afterimages. This is because real objects remain fairly stable on the retina when pursued, and thus pursuit would provide a much weaker cue than saccades that the afterimage is illusory. Using the terminology of Coren and Porac (1974), pursuit eye movements do not produce a decorrelation of the retinal image from the eye movement signal. Afterimages have often been used to study pursuit eye movements (e.g.efferent signals in the dark, Heywood & Churcher, 1971) but fewer studies have explored the effect of pursuit eye movements on afterimages. Those who have explored this have reported that afterimages move with the eyes during pursuit, but do not tend to disappear (Darwin & Darwin, 1786; Fiorentini & Mazzantini, 1965).

Saccade and context interactions

We have argued that the signals representing an afterimage are inherently ambiguous, and have suggested two cues that could influence the perceptual interpretation of these ambiguous signals. Consistent contexts, such as luminance edges, will shift the

interpretation in favour of the afterimage representing a real object, while saccadic eye movements will favour the interpretation that the afterimage is illusory. Figure 3.1 shows three predictions for how these cues could be combined to influence afterimage duration. The effect of context and saccades could be additive (a), and afterimage duration is increased by the presence of a contour and also decreased during saccadic eye movements. Alternatively, the cues could be combined in a 'winner takes all' approach, in which either the influence of the contour dominates the perceptual interpretation (b) or the influence of saccades does (c).

Phys

a   b   c
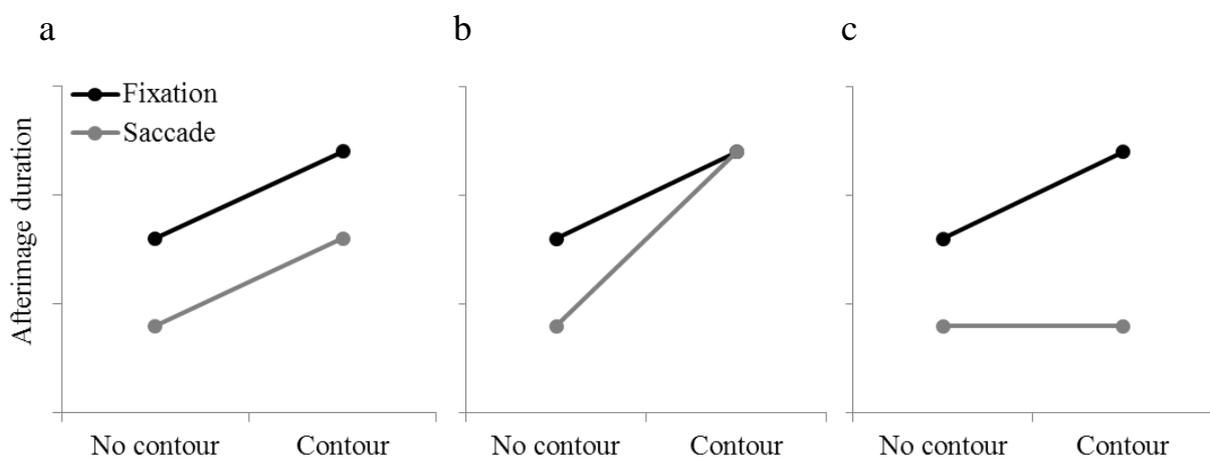
Figure 3.1. Three predictions for how context (luminance contour) and saccadic eye movement cues could be combined in their effect on afterimage duration. In (a) the effect of the context and the saccades are additive – the contour increases afterimage duration, while the saccade concurrently decreases it. In (b-c) one cue dominates the perceptual interpretation and determines the duration of the afterimage In (b) the contour dominates perceptual interpretation and afterimage duration remains the same during saccades as fixation, and in (c) the saccade cue dominates the perceptual interpretation and afterimage duration is reduced relative to fixation, even if a contour is presented.

The present experiments

The experiments in this chapter aim to confirm the finding that saccades suppress afterimage perception relative to pursuit and fixation. Unlike previous studies however we used short adaptation durations that are closer to the kind of fixation durations that often occur in real life. We also tested the context and eye movement interactions we predicted above, to find out whether context and saccades are combined in their influence on afterimages, or if one cue dominates the perceptual interpretation.

Experiment 3.1 measured the duration of colour afterimages under conditions of fixation, saccades and pursuit, and when the afterimage was framed, or not, by a luminance contour. Experiment 3.2, explored the effect of different saccade frequencies on afterimage perception, and also measured, alongside duration, the likelihood that the afterimage is perceived at all (in order to distinguish absent afterimages effects from short afterimages). Experiment 3.3 investigated whether blinks of different frequencies led to a reduction in afterimage perception. A similar suppression mechanism operates during blinks as during saccades, and blinks are also accompanied by changes in retinal illumination. However, unlike saccades, blinks do not decorrelate the retinal image of the afterimage with the eye/lid movement signal as movements of the eyes during blinks are small and slow (Gandhi & Katnani, 2011; Iwasaki et al., 2005). Experiment 3.4-5 explored whether misalignment of the contour with the afterimages, due to inaccurate fixation, influences how the contour interacts with different eye movement conditions. In Experiment 3.4 we introduced a degree of contour-afterimage misalignment that would be expected from the saccade condition into the fixation and pursuit conditions. In Experiment 3.5, we measured the degree of contour enhancement of the afterimages in the fixation and saccade condition but the contour was gaze contingent, thus reducing the consequences of inaccurate fixation.

Experiment 3.1: Afterimage duration during fixation, pursuit and saccades

Experiment 3.1 directly compared the effect of fixation, saccade and pursuit eye movements on colour afterimage duration, under conditions where a luminance contour framed, or did not frame, the afterimage. Duration was selected over other measures such and nulling and matching, because it is easier to equate across eye movements conditions (i.e. a null or match would also have to move with the eyes). Kennard et al., note that afterimages completely disappear when saccade frequency is above 2 per second. We used a saccade frequency of 1.67Hz (one every 600 ms) because we were interested in the total time taken for the afterimage to fade completely rather than any transient reduction in afterimage visibility due to saccadic suppression.

Observers viewed afterimages under three conditions of eye-movement: saccades, sinusoidal pursuit, and fixation (no eye movement). Observers followed a small dot to produce the eye movements. In the saccade condition, the dot jumped from side to side repetitively. In the pursuit condition, the dot translated sinusoidally from side to side. In the fixation condition, the dot remained stationary. A luminance contour was presented around the afterimage on half of the trials to explore an interaction with eye movement conditions. Observers were asked to respond when they perceived that the afterimage had completely faded, which was taken as a measure of afterimage duration.

Eye movement amplitudes of both 16° (Experiment 3.1a) and 8° (Experiment 3.1b) were tested. Previous studies have reported afterimage suppression at saccade amplitudes as low as 1°, so we were confident that we would be able to observe an effect of saccades with amplitudes of 8° and above. The experiment was conducted on a uniform grey background (CRT monitor) in a dark laboratory, thus minimising changes in luminance and background context at different points in the eye movement. The only context that did move was the luminance contour, but as this was always consistent with the eye movements it would act to enhance the afterimage rather than inhibit it.

The theory suggested by Exner predicts that saccadic eye movements will reduce afterimage duration relative to fixation and pursuit conditions. These results are expected because afterimages move with the eyes during saccades in a way that is unlike real objects, and thus will be suppressed. Based on the results of Chapter 2, we predicted that the luminance contour would increase afterimage duration in the fixation condition. Although in Chapter 2 we measured saturation of afterimages and not duration, it is likely that they are related. We predicted the effect of the contour on the afterimages in the saccade conditions would follow one of the three patterns shown in Figure 3.1: an additive effect of both cues (a), or one cue dominating perception (b-c).

Methods

Observers

Six observers (five naive, one author; 3 males, 3 females) participated in Experiment 3.1a, and eight observers (seven naive, one author; 6 males, 2 females) participated in Experiment 3.1b. Three observers participated in both Experiments. All had normal colour vision and normal or corrected-to-normal visual acuity.

Materials and Procedure

Apparatus is described in Chapter 2 and 3. The adapting stimuli were green (x = 0.252, y = 0.487, Y = 28.8) or pink (x = 0.303, y = 0.171, Y = 28.8) 3° diameter circles, presented 8° to the left or right of centre in Experiment 3.1a, and 4° to the right/left in Experiment 3.1b. Observers fixated a 0.15° dot in the centre of the adapting stimulus. The adapting stimulus was removed after 1.5 seconds, leaving the dot which was used to direct the eye movements. In the saccade condition, the dot continuously jumped from left to right of the screen every 600ms (1.67hz). In the pursuit condition, the dot smoothly and continuously translated (in a sinusoidal pattern) from left to right (frequency of 0.33Hz in both the 8° and 16° conditions). In the Fixation condition, the dot remained stationary (same location to adaptation) on either the left or the right of the screen. In Experiment 3.1a the amplitude of the eye movements was 16° (dot moved from + and − 8° of centre), in Experiment 3.1b the amplitude of eye movements was 8° (dot moved from + and − 4° of centre). Observers were instructed to remain carefully fixated on the dot at all times, even when it moved. Observers pressed a response box key when they perceived that the afterimage had completely faded, and all trials were terminated once a response was collected. To reduce carryover adaptation, the trials ended with a cycling coloured mask (described in Chapter 2). Example trials are shown in Figure 3.1.

There was a total of 18 trial types, within 2 (adaptation hue) x2 (adaptation side) x 2(contour presence) x 3 (eye movement condition) design. Eye movements conditions were blocked into three sessions, the remaining trial types were randomised within sessions. Observers received ten repetitions of each trial type in Experiment 3.1a and eight repetitions in Experiment 3.1b, totalling 40 and 32 repetitions for each eye-movement condition in Experiment 3.1a and b respectively.

Eye movement analysis

Eye movement traces were recorded with a CRS high speed video eye tracker sampling at 250hz and smoothed with a Gaussian filter (sd = 4Hz). The samples during the afterimage measurement phases were analysed to distinguish blinks from saccadic eye movements. Fixation and pursuit trials that contained saccades were discarded to reduce cross-condition contamination. Blinks were detected and the relevant samples screened from further analysis. Saccades were detected by calculating the 'jerk' at each point, which corresponded to the derivative of the eye acceleration (Wyatt, 1998). Samples were recorded as a saccade if the 'jerk' value exceeded a criterion of 30 deg/s^3. To estimate gaze precision, we calculated the standard deviations of the difference between gaze position and the dot that the observers were asked to follow. The accuracy measurements were based on the unfiltered eye traces, to remain consistent with previous analyses (e.g. Chapter 2). All eye movement traces and the output of the analysis were visually checked. Overall, very few fixation and pursuit trials were discarded because they contained saccades (less than 5%). This eye movement analysis was used throughout this chapter, unless stated otherwise.

a Fixation

Fixation 150ms

Adaptation 150ms

Duration measurement - fixation

Mask 600ms

b Saccade

Fixation 150ms

Adaptation 200ms

Duration measurement – saccade (600ms)

Duration measurement – saccade (600ms)

Mask 600ms

c Pursuit

Fixation 150ms

Adaptation 200ms

Duration measurement – pursuit (600ms)

Duration measurement – pursuit (600ms)

Mask 600ms
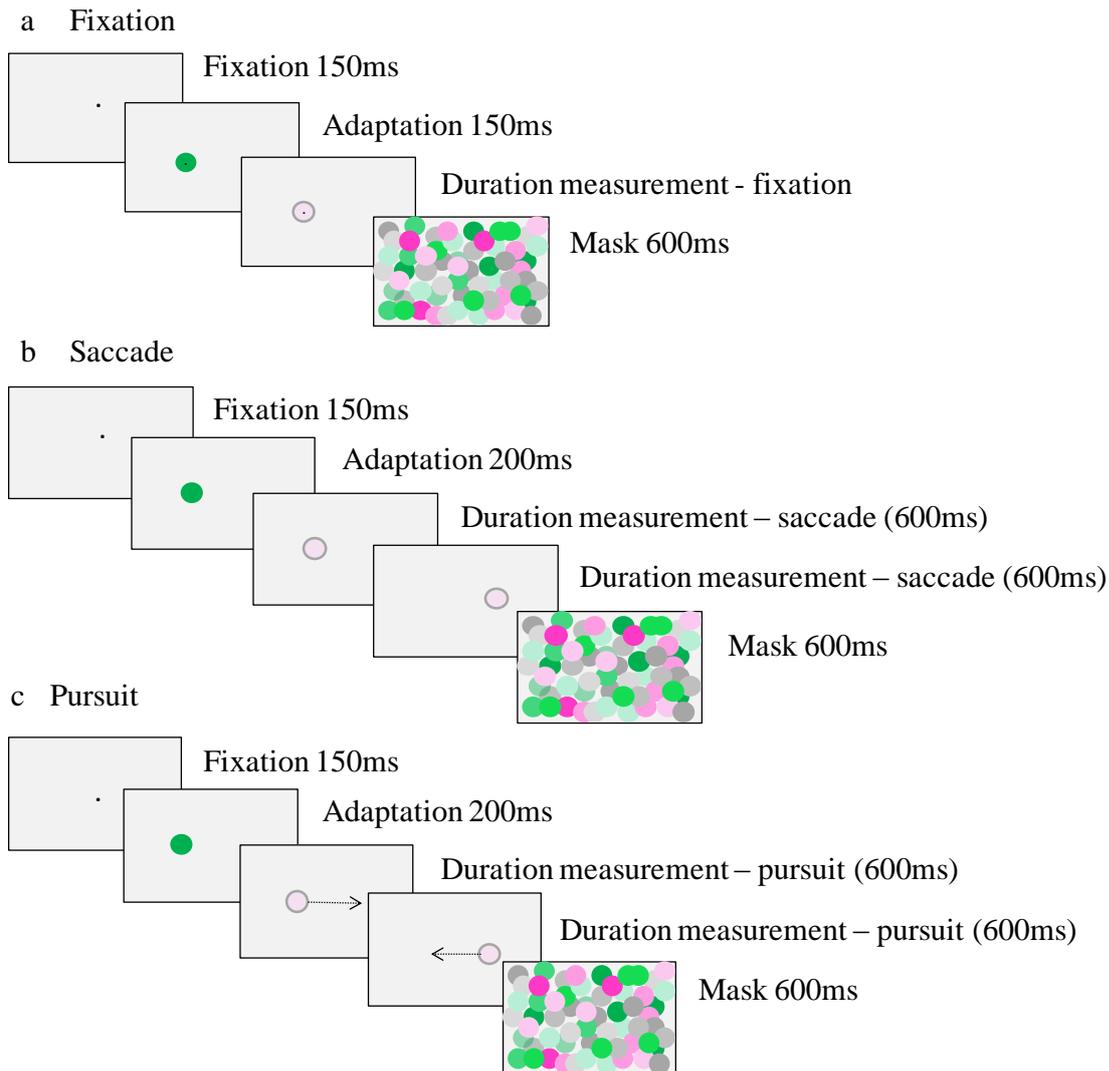
Figure 3.1. Example trials from Experiment 3.1. *(a) Fixation condition.* Observers acquire fixation on a black dot presented for 100ms either to the left or right of centre. A green or pink adaptation circle is then displayed for 150ms. This is then removed and the stable fixation dot remains. Observers remain fixated on the dot and press the response key when they perceive the afterimage has faded. Trials end with a 600ms cycling coloured mask. *(b) Saccade condition.* Fixation and adaptation is the same as in the fixation condition. After adaptation, the black dot jumps from the left (right) to right (left) every 600ms and observers press the response key when the afterimage has faded. *(c) Pursuit condition.* Fixation acquisition and adaptation as described above. After adaptation, the dot moves in a smooth, sinusoidal pattern from left (right) to right (left) until the response key is pressed to indicate the afterimage has faded. On half the trials for all conditions the black dot is surrounded by a luminance contour at all points during the afterimage measurement phase (contour not shown in this figure).

Results and discussion

A similar pattern between eye movement condition (fixation, saccade, pursuit) and contour presence was found for both Experiment 3.1a with 16° eye-movements (Figure 3.2a) and Experiment 3.1b with 8° eye-movements (Figure 3.2b). Afterimage duration did not appear to differ between eye-movements conditions when no contour was presented, but afterimage duration significantly increased in the fixation and pursuit conditions relative to the saccade conditions when a contour framed the afterimages (ANOVA on interaction from Exp 1a, $F(2, 10) = 4.36$, $p < 0.05$, and Exp 1b, $F(2, 14) = 17.75$, $p < 0.001$). Follow up tests on the interaction from Experiment 3.1a revealed that the contour increased afterimage duration in the fixation condition more than the saccade condition ($p < 0.05$). However, contour enhancement did not differ significantly between pursuit and saccade conditions ($p = 0.11$), or pursuit and fixation conditions ($p = 0.282$). For Experiment 3.1b the contour increased duration more during fixation than saccade ($p < 0.001$), and also more during pursuit than saccade ($p < 0.01$). Once again, contour enhancement did not significantly differ between pursuit and fixation ($p = 0.282$).
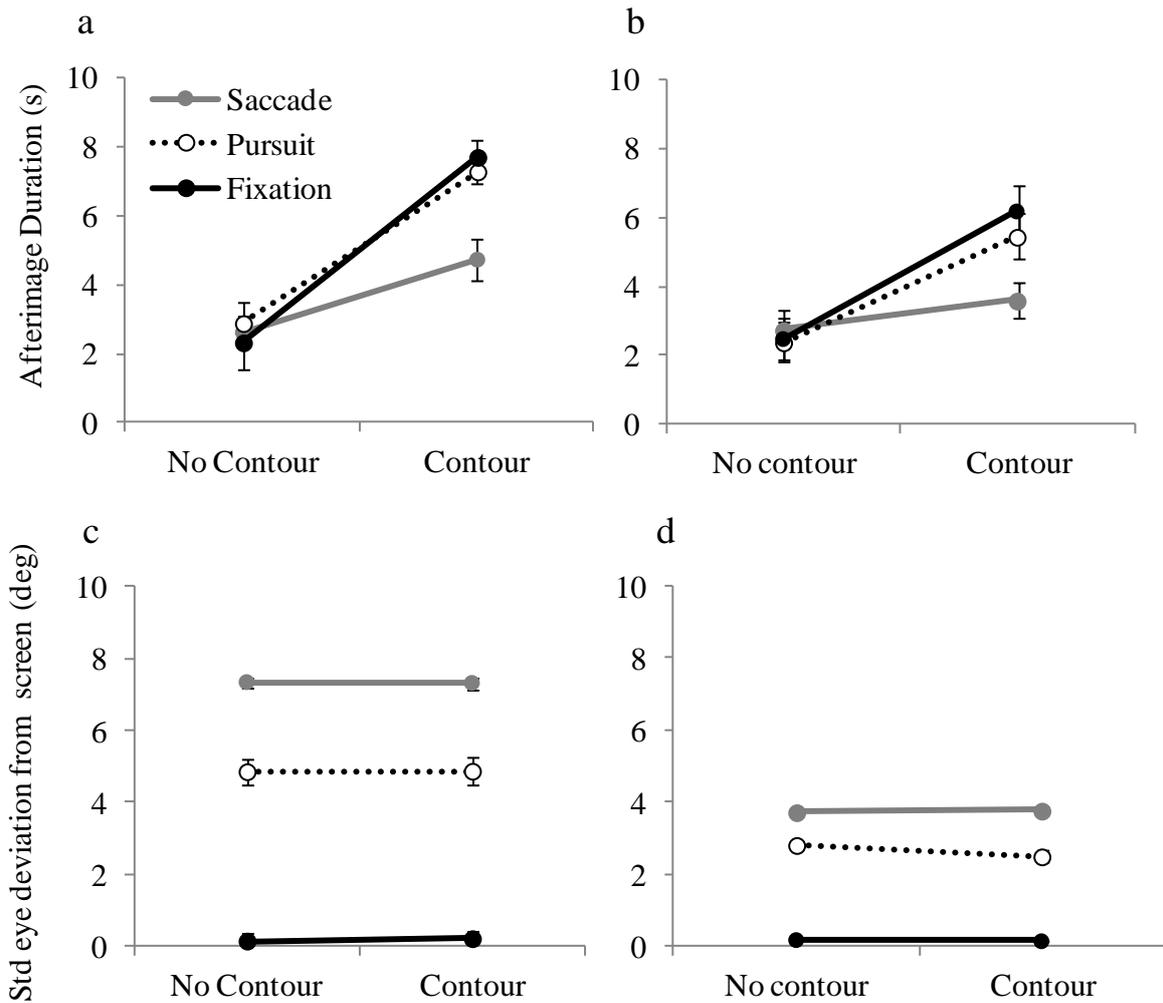
Figure 3.2. Duration results from Experiment 3.1a with 16deg eye movements (a) and 1b with 8deg eye movements (b). Mean afterimage duration across observers is plotted against the contour and no contour conditions. Eye-movement conditions are shown as separate lines: fixation (black), pursuit (dotted) and saccade (grey). Both Experiment 3.1a and 1b show a similar interaction: little difference is observed between the eye-movement conditions when no contour is present, but afterimage duration is increased in the fixation and pursuit conditions relative to the saccade condition when a contour is present. **Deviation of eye position from screen position of the dot observers were asked to fixate for Experiment 3.1a(c) and Experiment 3.1b(d).** For both experiments, standard deviation is larger in the saccade condition than pursuit and fixation, and larger in pursuit than fixation. This suggests that the contour is misaligned with the afterimage more in the saccade condition than the pursuit and fixation, and more during pursuit than during fixation. Deviation during fixation and pursuit is larger in Experiment 3.1a where the eye movement amplitudes were larger than in Experiment 3.2b. Error bars show, for each condition, the standard error of the differences from each participant's mean.

These results are consistent with our hypothesis that afterimages during pursuit and fixation would be of similar duration, both when a contour was present and when it was not present. We also expected that the contour would lead to an increase in afterimage duration in the fixation and pursuit conditions, and indeed, this is what was found. However, there are two findings that require further investigation. First, we predicted that saccades would reduce afterimage duration when no contour was present relative to fixation and pursuit conditions. Our findings are inconsistent with the majority of previous research reporting that saccades reduce the duration of afterimages and other stabilised images (Coren & Porac, 1974; Ferree, 1908; Fiorentini & Mazzantini, 1965; A. H. Friedman & Marchese, 1978; Helmholtz, 1962; Kennard et al., 1970) (Darwin & Darwin, 1786; Yarbus, 1967). They also do not support the hypothesis that because afterimages move with the eyes unlike real objects, saccades provide evidence that the afterimages are illusory and this leads to their suppression (Exner, 1890). We will explore this unexpected finding further in Experiments 2-3.

Second, the finding that there is less relative enhancement of afterimages by the contour in the saccade condition than in the pursuit or fixation conditions, could suggest that the saccade cue dominates the perceptual interpretation of whether to perceive the afterimages (e.g. the results are similar to Figure 3.1c). However, the alternative explanation is that the smaller degree of contour enchantment in the saccade condition is due to a greater degree of contour-afterimage misalignment during saccades. This possibility is reflected in the difference across eye movements conditions in the standard deviations in eye movement position from screen fixation dot in Experiment 3.1a (Figure 3.2c) and 1b (Figure 3.2d). For both Experiments, there is a much larger deviation in the saccade condition than fixation, and also a larger deviation in during pursuit than fixation. This means the contour would have been less aligned with the afterimage during saccades than during fixation, and to a lesser extent, during pursuit than during fixation. This explanation is explored further in Experiment 3.4-5.

Experiment 3.2: Why did saccades fail to suppress afterimages?

A floor effect could explain why saccades did not decrease afterimage duration when no contour was present in Experiment 3.1 as the afterimages lasted only around 2s. Experiment 3.2a was a replication of the saccade and fixation conditions of Experiment 3.1b. However, before commencing the main experiment we increased the adaptation duration in a pilot to produce substantially longer afterimage durations and re-examined the influence of saccades. We also added an 'I did not see an afterimage' response option, which allowed us to distinguish very short afterimage durations from the time taken to respond when no afterimage was seen at all.

We were also interested in whether faster saccade frequencies would result in shorter afterimage durations. Kennard et al.,(1970) reported that afterimages completely disappeared during periods of fixation when saccade frequencies were above 2Hz. Saccade frequency was 1.67Hz in Experiment 3.1, thus we were not expecting the afterimages to disappear immediately on every trial and remain suppressed. However, it is possible to argue that a saccade frequency of 1.67Hz contained fixation periods that are so long they underestimated the effect of the saccades. Experiment 3.2a therefore compared a faster saccade frequency of 3.34Hz to the original saccade frequency of 1.67Hz. A possible outcome of using a faster saccade frequency is that the afterimages would be trapped within a loop of continual saccadic suppression and could not be seen at all. If this is the case we would not expect to collect any duration measurements for the fast saccade condition, only responses that the observer did not see an afterimage at all.

The motivation of Experiment 3.2b to test whether the lack of difference between pursuit and fixation (without a contour) in Experiment 3.1 could be attributed to a floor effect, rather than as support for our hypothesis that duration during pursuit and fixation should not differ. The design of Experiment 3.2b was a replication of a pursuit and fixation conditions from Experiment 3.1b, but with the addition of (a) a pilot to insure fixation afterimage duration were above 4s, and (b) an 'I did not see an afterimage' response option.

Methods

Observers

Seven observers (six naive, one author; four males, three females) participated in Experiment 3.2a and seven observers (six naive, one author; four males, three females) participated in Experiment 3.2b. All had normal colour vision and normal or corrected-to-normal visual acuity.

Pilot to ensure duration of baseline fixation afterimages was above 4s

Before participating in Experiment 3.2a-b, all observers completed a short pilot to ensure their baseline fixation condition afterimages (no contour present) were 4s in duration or above. Afterimage duration was controlled by increasing the duration of the adapting stimulus with a staircase design. Observers fixated centrally and were adapted to either a pink or green circle (see Chapter 2 for description). Initial adaptation was set to 2s. They were then asked to respond when the afterimage had faded. The staircase adjustment began after the first five trials, and terminated once four consecutive afterimage durations of 4s or above were recorded. If the afterimage duration was less than 4s, 250ms of additional adaptation was added to the next trial. If observers failed to reach four consecutive afterimage durations of 4s when adaptation duration reached 6s, the pilot was terminated. We set this limit as adaptation durations above 6s in the main experiments would reduce the quality of the eye movements (i.e. by increased blinking and discomfort). One observer in Experiment 3.1failed to reach the criterion of 4s and so was tested with an adaptation duration of 6s.

Stimuli and procedure

For Experiment 3.2a (saccades vs fixation), stimuli and procedure were the same as the fixation and saccade conditions of Experiment 3.1b, apart from a few differences. First, no contour was presented at any point. Second, the fixation dot jumped from side to side at two different frequencies: 1.67Hz (replication of Exp 1b) and 3.34Hz. Third, in addition to signaling when the afterimage faded, observers were also given an 'I did not see an afterimage at all' response option.

There was a total of 12 trial types, within 2 (adaptation hue) x 2 (adaptation side) x3 (eye movement condition) design. Eye movements conditions were blocked into three sessions, the remaining trial types were randomised within sessions. Observers received eight repetitions of each trial type, totalling 32 repetitions for each eye movement condition.

For Experiment 3.2b (pursuit vs fixation), stimuli and procedure were exactly the same as the no-contour fixation and pursuit condition from Experiment 3.1b, with the addition of the pilot and the 'I did not see an afterimage' response.

There was a total of 12 trial types, within 2 (adaptation hue) x 2 (adaptation side) x 3(eye movement condition) design. Eye movements conditions were blocked into three sessions, the remaining trial types were randomised within sessions. Observers received eight repetitions of each trial type, totalling 32 repetitions for each eye movement condition.

Results and discussion

As seen in Figure 3.3a, we now find the predicted result that saccades reduce afterimage duration relative to fixation (ANOVA main effect: $F(2, 12) = 11.44$, $p < 0.01$; comparisons between fixation and 1.67 and 3.34Hz saccade frequency both $p < 0.05$). This effect increased with the frequency of the saccade; afterimage durations during 1.67Hz saccades were significantly longer than during 3.34Hz saccades ($p < 0.05$). The difference between fixation and saccade conditions is also reflected in the finding that observers are more likely to see the afterimage in the first instance in the fixation condition than the saccade conditions (ANOVA main effect: $F(2, 12) = 4.29$, $p < 0.05$, comparisons between fixation and slow and fast saccade both $p < 0.05$). There was no significant difference in the percentage of trials where an afterimage was seen between the 3.34 and 1.67Hz saccades (Figure 3.3b, $p = 0.31$).

Figure 3.3c shows that there was no significant difference between afterimage duration during fixation and pursuit eye movements ($t(6) = 1.2$, *n.s.*). There was a slight trend for pursuit durations to be lower than fixation durations, in all but two observers. Thus, in order to compare the results of Experiment 3.2a and 2b, we normalised the saccade and pursuit durations on their respective fixation conditions. We found that the reduction in afterimage duration from the baseline fixation condition was significantly larger during saccades (Experiment 3.2a) than pursuit (Experiment 3.2b), for both 1.67Hz saccades ($t(6) = 3.6$, $p <$

0.01) and 3.34Hz saccades ($t(6) = 4.06$, $p < 0.01$). The percentage of trials where an afterimage was seen across fixation and pursuit conditions did not significantly differ ($t(6) = 1.5$, *n.s.*) and unlike the duration measure, there was no convincing trend towards a difference (Figure 3.3d).
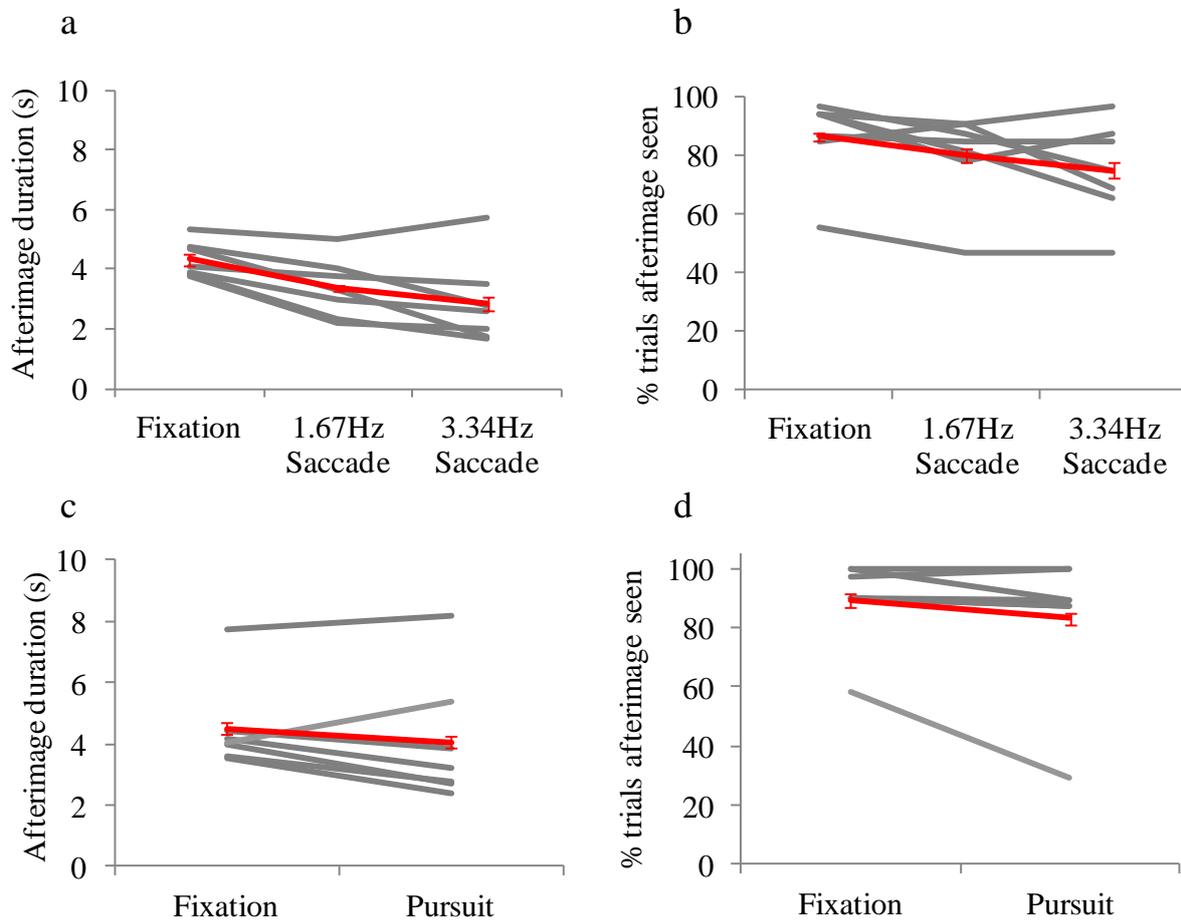
Figure 3.3. Results from Experiment 3.2a with saccades (a-b) and Experiment 3.2b with pursuit (c-d). (a) Afterimage duration in fixation, slow saccade and fast saccade condition across individual observers (grey lines) and their mean (red line). Afterimage duration decreases in the saccade conditions relative to fixation, and duration for 3.34Hz saccades is shorter than for 1.67Hz saccades. (b) Percentage of trials where an afterimage was seen is higher in the fixation condition than either saccade condition. (c) Afterimage duration in fixation and pursuit conditions. Durations are similar across fixation and pursuit, although there is a non-significant trend that pursuit durations are shorter than fixation. (d) For most observers, the percentage of trials where an afterimage is seen is similar across pursuit and fixation conditions.

The results from Experiment 3.2 are more consistent with previous findings that saccades reduce afterimage duration relative to fixation. We did not find a significant difference between fixation and pursuit, although there was a trend for durations to be lower during pursuit than fixation. However, comparison between saccades and pursuit suggests that even if pursuit reduces afterimage durations it is unlikely to be to the same extent as saccades.

Taken together, these results are consistent with Exner's (1890) theory that saccades offer a means of disguising an illusory, stabilised image from a real object in a way that fixation and pursuit cannot. Saccades at faster frequencies may boost this effect because they increase the number of saccades per second, thus increasing the amount of evidence accumulated per second that the afterimage is a feature of the eye, not of the world. Saccadic suppression is unlikely to account for this finding because overall afterimage duration is reduced, not just a temporary suppression around the time of the saccade. Furthermore, as we minimised the context and illumination changes during eye movements by using a uniform background, we are confident that changes in context theories are also unlikely to explain our results.

The possibility remains that the physiological effects of the eye muscle movements themselves could influence the perception of the afterimage (Flick and Gurber, 1889, as cited by, Exner, 1890; Matin, 1974) Thus, in order to confirm that it is the lack of positional change of the afterimage after a saccade that primarily drives their suppression, we devised a control experiment that would produce (a) similar suppression to saccadic suppression, (b) changes in illumination on the retina, and (c) some contractions of the extraocular muscles, but all without the positional conflict of afterimages and saccadic eye movement signals. The way to accomplish this was to measure afterimage duration during repetitive blinking.

Experiment 3.3: Blinks as a control for retinal state theories

Blinks and saccades are probably generated independently but share the same basic ocular motor systems (Bodis-Wollner, Bucher, & Seelos, 1999; Bour, Aramideh, & Ongerboer De Visser, 2000; Bour, de Visser, Aramideh, & Speelman, 2002; Gandhi & Katnani, 2011). Voluntary blinks produce suppression that is extremely similar to saccadic suppression in both magnitude and time course (Burr, 2005; Ridder III & Tomlinson, 1993, 1997; Volkmann, Riggs, Ellicott, & Moore, 1982). Both blink suppression and saccadic suppression are likely to arise from similar processes, involving the use of efferent signals about an imminent saccade or blink to suppress retinal signals around the time of the eye or lid movement (Bristow, Haynes, Sylvester, Frith, & Rees, 2005; Stevenson, Volkmann, Kelly, & Riggs, 1986). One argument is that blink suppression is due to eye movements that accompany blinks. When centrally fixated, the eyes loop downward and nasally during each blink before returning to fixation (Gandhi & Katnani, 2011; Iwasaki et al., 2005). These movements tend to be small and are due to either lid pressure on the eyeball, or more probably, co-contraction of the extraocular muscles (Bergamin, Bizzarri, & Straumann, 2002; Collewijn, van der Steen, & Steinman, 1985; Evinger, Shaw, Peck, Manning, & Baker, 1984; Gandhi & Katnani, 2011; Ginsborg, 1952; Ginsborg & Maurice, 1959; Volkmann et al., 1982). However, they are too slow to be considered saccades (Collewijn et al., 1985; Gandhi & Katnani, 2011; Riggs, Kelly, Manning, & Moore, 1987), thus it is likely that blink suppression involves mainly blink-specific mechanisms (Ginsborg, 1952; Ginsborg & Maurice, 1959; Volkmann et al., 1982).

Although blinks do not produce smearing of the visual field, they do produce a varying change in retinal luminance as the eye lids close and open. Blinks also produce some contractions of the extraocular muscles and increase IOP levels (Murgatroyd & Bembridge, 2008). Contractions during blinks may not be of the exact same magnitude and muscle fibre or motor neuron origin as those that generate saccadic eye movements. However, evidence from clinical disorders suggests that they share some physiological similarities (Leigh, Newman, Folstein, Lasker, & Jensen, 1983; Zee et al., 1983). Critically for our argument, blinks do not decorrelate the eye movement (or 'blink') signal from the retinal image, thus, like fixation and pursuit, are not a cue to the visual system that the afterimage is moving unlike a real object.

One possible concern for using blinks as a control for saccades is that intense positive afterimages produced by high luminance adapters are still visible during blinks, while real objects will disappear from view. However, in our experiments we used fairly low luminance adapting stimuli that would not be sufficient to maintain a positive afterimage during the blink.

There is little previous research exploring the effect of blinks on afterimages. Some authors have compared them to saccades and advised that blinking is avoided during afterimage experiments (Helmholtz, 1962; Kennard et al., 1970). Others have suggested that blinks may bring back the afterimage percept once it has faded (Brindley, 1962; Troland, 1917; Newton, as cited in, Wade, 2000; Wang, Munch, Hasler, Prünte, & Larsen, 2008). However, as far as we are aware, no one has directly explored the effect on repetitive blinking on afterimage duration.

Experiment 3.3 was a replication of Experiment 3.2a but observers continually blinked in response to auditory cues instead of performing saccades to fixation points. Observers either fixated with eyes open, fixated and made slow frequency blinks (1.67Hz), or fixated and made fast frequency blinks (3.34Hz). We repeated the pilot from Experiment 3.2 to ensure that the baseline fixation afterimage duration was 4s or above to avoid floor effects. Based on Exner's theory we predicted that afterimage duration would be similar for blink and fixation conditions, because blinks, like fixation, cannot distinguish an afterimage from a real stimulus. Saccadic suppression and changes to the retinal state theories would predict that blinks should produce a similar reduction in afterimage duration as saccades.

Methods

Observers

Seven observers (six naive, one author; four males, three females) participated in Experiment 3.3. All had normal colour vision and normal or corrected-to-normal visual acuity.

Stimuli and procedure

Observers first completed the pilot described in Experiment 3.2, to increase adaptation duration until fixation afterimages were 4s or above. Stimuli and procedure for Experiment 3.3 were the same as Experiment 3.2, apart from a few differences. The fixation dot always remained in the centre of the screen. During the afterimage measurement stage, observers were instructed to blink in response to a 0.1s low frequency tone. In the slow blink condition the tone was played every 600ms (1.67Hz blinks frequency); while in the fast blink condition the tone was played every 300ms (3.34Hz blinks frequency). In the fixation condition no tones were played. Observers were instructed to avoid blinking unless a tone was played. The contour was not presented at any point. As in previous experiments, observers were instructed to respond when the afterimage had completely faded, or press a separate response key if no afterimage was seen at all.

There was a total of 6 trial types, within 2 (adaptation hue) x 3 (blink condition) design. Blink conditions were blocked into three sessions, the remaining trial types were randomised within sessions. Observers received 20 repetitions of each trial type, totalling 40 repetitions for each blink condition.

Results and discussion

Figure 3.4a shows an inconsistent pattern of afterimage durations in the fixation and high frequency and low frequency blink conditions across observers. Overall, these differences were not significant ($F(2, 12) = 0.67$, *n.s.*), suggesting that there is little consistent evidence that blinks reduce afterimage duration relative to fixation. A similar result was found for the number of trials where no afterimage was seen, where there were also no significant differences between conditions ($F(2, 12) = 2$, *n.s*). In order to directly compare the effects of saccades and blinks, we normalized the saccade condition duration from Experiment 3.2a and blink durations from this experiment on their respective fixation durations. This was done by taking the difference in duration between the fixation baseline durations and blink and saccade durations for each observer. Comparison of these differences revealed that the difference in afterimage duration between the saccade and fixation conditions was larger than between the blinks and the fixation condition, for both the 1.67HZ conditions ($t(6) = 2.73$, *p* < 0.05) and the 3.34Hz conditions ($t(6) = 4.25$, *p* < 0.05).

Blinks produce similar conditions to saccades, including suppression, a certain degree of extraocular muscle contraction and changes in retinal illumination, yet the results from this experiment suggest that they do not reduce afterimage perception to the same extent as saccades. One explanation for this finding is that blinks do not produce a conflict between the eye movement signals and the retinal position of the afterimage. Given the similarities between blink suppression and saccadic suppression (Burr, 2005; Ridder III & Tomlinson, 1993, 1997; Volkmann et al., 1982), we would expect to find a similar reduction in afterimage duration after blinking as we find with saccades if saccadic suppression is the primary reason for lower afterimage durations during saccades.

Blinks are not the 'perfect' control for saccades because they unable to account for all of the changes that occur during a saccade. However, they produce similar effects to saccades in terms of the theories that have previously been put forward for why saccades reduce afterimage perception (saccadic suppression, vascular changes). There are, however, other differences between saccades and blinks. For example, saccades produce a compression of space and time which may not occur for blinks (Morrone, Ross, & Burr, 2005; Ross, Morrone, & Burr, 1997). However, there is no obvious theoretical reason for how these compression effects would influence the intensity of afterimage signals.
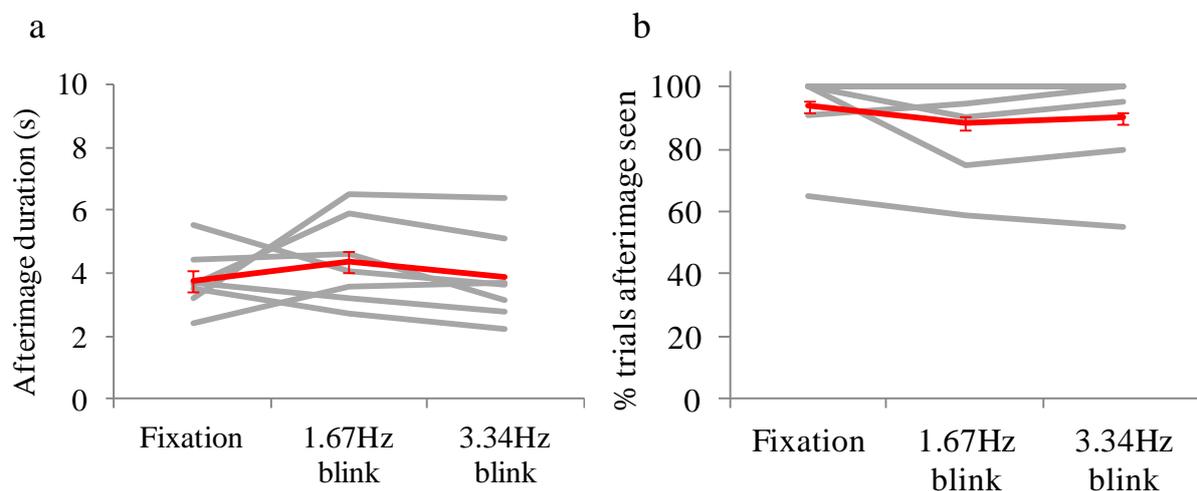
Figure 3.4. Results from Experiment 3.3. (a) Mean afterimage duration for each observer (grey lines) and the mean across observers (red line) for fixation condition and slow and fast blink conditions. There is no evidence that afterimage duration reduces (or increases) in the blink conditions relative to fixation. (b) Percentage of trials where an afterimage is seen does not appear to differ across fixation and blink conditions.

Experiment 3.4-3.5: Contour and eye movement interactions

In Experiment 3.1, we were interested in how different cues that modulate the ambiguity of an afterimage would interact. We predicted that either the effect of the contour and saccades would be additive (Figure 3.1a), or one cue would dominate the perceptual interpretation more than the other (Figure 3.1b-c). In Experiment 3.1, we found that the contour enhanced afterimages during fixation and pursuit more than during saccades. This suggests that the saccades influenced afterimage durations more than the contour.

However, before concluding that this is the nature of saccade-contour interactions, we explored some lower-level explanations for why the contour may have been less effective at enhancing the afterimages during saccades than during fixation or pursuit. First, it is possible that the contour is less consistently aligned with the afterimage in the saccade condition than in fixation/pursuit conditions. This is because gaze position is less accurate during saccadic eye movements than during fixate or pursuit (see Figure 3.2c-d). First, the eyes need time to acquire fixation after each saccade, during which small corrective eye movements occur. During these corrective movements, the afterimage is no longer directly aligned with the contour, which could reduce the ability of the contour to enhance the afterimage. Second, even though the saccades were predictable, observers rarely move in perfect time with the fixation dot and contour movement and are either early or late in making a saccade. In both situations, there is a short interval where the eyes are directed to the opposite side of the screen to the contour, during which the afterimage is not aligned with the contour and does not benefit from its enhancement.

Hence, in Experiment 3.4 and 3.5 we aimed to equate the amount of time the afterimages were aligned with the contour across fixation, pursuit and saccades conditions. Once equated, we were interested in whether the contour still enhanced afterimages less during saccades than during fixation/pursuit.

Experiment 3.4: Introduce saccade-like jitter to fixation and pursuit

In Experiment 3.4, we designed a fixation and pursuit condition that included a similar degree of contour misaligned to the saccade condition. In order to achieve this, we used eye movement data from the saccade condition in Experiment 3.1b to calculate the exact profile of contour misalignment for each trial, and for each observer, and added this jitter to the contour in the fixation and pursuit conditions. Thus, the animated jitter of the contour mirrored the jitter produced by that observer during saccade trials in Experiment 3.1b. Furthermore, to mimic saccadic suppression effects, we turned off the contour for the duration of each saccade recorded in Experiment 3.1b. In Experiment 3.4a, we reproduced the jitter in its entirely, including saccadic latencies and premature saccades (Experiment 3.4a). This resulted in some large contour movements, up to 8° away from the fixation point. To investigate the influence of these large movements, in Experiment 3.4a we edited the jitter so that these large movements due to saccade latencies and premature saccades were removed (Experiment 3.4b). This left a smaller degree of jitter that was due to corrective saccades and other small movements. The latter condition was included as we assumed that very large contour movements might be distracting for observers, and could produce saccades towards the contour and away from the fixation point, thus contaminating the fixation and pursuit trials with added saccades.

Methods

Observers

The same observers participated in Experiment 3.4 as participated in Experiment 3.1b, as individual contour jitter was calculated for each observer based on their eye movement data.

Calculation of contour jitter

Eye movement data collected from saccade trials for each observer from Experiment 3.1b was analysed. For each eye tracker sample point on each trial, the difference between the eye movement position and screen location of the contour was calculated separately for horizontal and vertical eye movements. This data was then sampled at the refresh rate of the monitor (100hz), and used to position the contour on the screen. Periods during a saccade were identified based on eye movement speeds above 10° per sec and a position change

during this time of more than 2°. The contour was turned off during these periods, to simulate saccadic suppression effects. Because afterimage durations were shorter in the saccade condition than the fixation and pursuit conditions, we had to allow for the possibility that there may not be enough eye-tracking data on each trial to insert into the fixation and pursuit conditions. Thus, initially we used the exact eye movement sequence from each saccade trial. If a given trial proved to be longer than this, we filled the remaining time with a random selection of 600ms snippets yoked from other trials. These snippets each started with a saccade and covered the fixation period after that saccade up until the point of the next saccade. This was done both for the contour jitter locations and for the saccadic suppression intervals when the contour was switched off.

Experiment 3.4a, used the whole gamut of contour locations, including those that represented saccade latencies and premature saccades which produced a large contour offset. In Experiment 3.4b, the contour was turned off during any contour jitter offsets that were greater than 1deg in any direction, to stimulate the misalignment of the contour with the afterimage but to avoid the observers making saccades to the jumping contour.

Stimuli and Procedure

Stimuli and procedure was the same as Experiment 3.1b with the exception of extra contour jitter introduced into the fixation and pursuit conditions. We did not re-run the saccade condition. To remain consistent with Experiment 3.1b, we only recorded duration measurements not the number of trials where no afterimage was seen.

For both Experiment 3.4a and 3.4b, there was a total of 6 trial types, within 2 (adaptation hue) x 2 (adaptation side) x 2 (eye movement condition) design. Eye movements conditions were blocked into two sessions, the remaining trial types were randomised within sessions. Observers received 20 repetitions of each trial type, totalling 40 repetitions for each eye movement condition.

Results and Discussion

Figure 3.5a shows the original interaction from Experiment 3.1b, whereby the contour increased duration more in fixation and pursuit conditions than the saccade condition. Figure 3.5(b-c) shows results from Experiment 3.4 where jitter was introduced to fixation and pursuit conditions to mimic misalignment of contour and afterimage during the saccade condition. Large jitter with offsets from saccade latencies and premature saccades is shown in Figure 3.5b, while jitter with these large offsets removed is shown in Figure 3.5c.

The comparison we are interested in is whether the durations of pursuit and fixation in the contour conditions plus added jitter are reduced to the level of the contour-saccade condition from Experiment 3.1b or remain relatively higher. A reduction would suggest that the saccade did not bias the perceptual interpretation of the afterimage more than the contour in Experiment 3.1, but rather, the contour was less salient in the saccade condition because it was less aligned with the afterimages. If the pursuit and fixation contour effect in this experiment remain higher than the saccade contour effect in Experiment 3.1, this would suggest that the saccade influences the perception of the afterimages more than the contour, and this effect is not related to the misalignment of the contour in the saccade condition.

No significant contour effect was found for either fixation or pursuit in the large jitter condition ($F(1, 7) = 1.51$, *n.s*; interaction is also not significant, $F(1, 7) = 3.88$, *n.s.*). However, the contour did significantly increase afterimage duration for both fixation and pursuit in the small jitter condition ($F(1, 7) = 6.26$, $p<0.05$; interaction non-significant, $F(1, 7) = 1.03$, *n.s.*). Replicating the results of Experiment 3.1 and Experiment 3.2b, we found no significant difference between pursuit and fixation in any conditions (no main effect of eye movement in small jitter condition $F(1, 7) = 1.89$, *n.s.*, and large jitter condition, $F(1, 7) = 0.39$, *n.s.*).

In order to directly compare the effect of the contour in the fixation and pursuit conditions from Experiment 3.4 and the saccade condition from Experiment 3.1b, we calculated degree of contour enhancement for each condition by taking the difference between their no contour and contour durations (data not shown). Two one-way ANOVAs conducted on these differences revealed that the contour effect for the saccade condition in Experiment 3.1b is

similar to the contour effects we found for pursuit and fixation in both the small jitter ($F(2, 14) = 0.77$, *n.s.*) and large jitter ($F(2, 14) = 2.39$, *n.s.*) conditions. These comparisons suggest that the decrease in the contour effect in the saccade condition in Experiment 3.1 may be a consequence of greater contour misalignment with the afterimages rather than the saccade cue dominating perception of the afterimages.
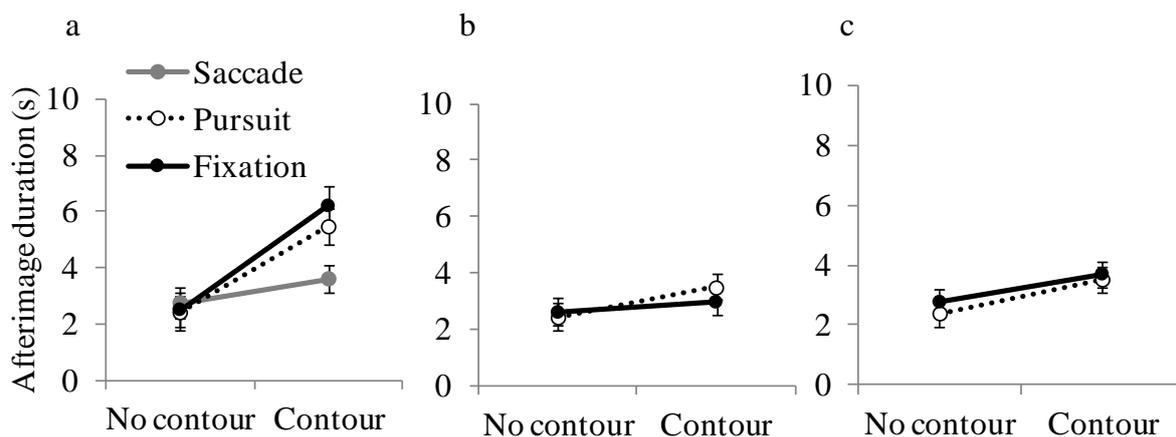
Figure 3.5. Results from Experiment 3.1b (a), Experiment 3.4a with large contour jitter (b) and 3.4b with small contour jitter (c). Afterimage duration in the fixation (black) and pursuit (white, dotted) conditions is not increased by the contour as much when contour jitter is present (b-c) that when it was not present (a). This effect is particularly pronounced in the large jitter fixation condition, where the contour did not increase afterimage duration at all.

Figure 3.6 shows that the accuracy of the gaze position is better during fixation than pursuit, for both the large jitter (a) and small jitter (b) conditions, and regardless of whether a contour is presented. This pattern is consistent with the accuracy measurements reported in Experiment 3.1. The consequence of this is that the contour would not have been aligned with the afterimage as much during pursuit as during fixation. Thus, it is possible that the contour enhancement for afterimages during pursuit may be an underestimation compared to a situation where gaze was more accurate. It is unclear why, given that the contour effect for pursuit may be underestimated, the contour effect for pursuit and fixation have been consistently similar across experiments. We could speculate from this that the contour is more effective during pursuit than fixation, thus is capable of enchaining the afterimages to the same extent as fixation despite being proportionally less aligned with the afterimages. One possible reason for this is that sensitivity to high spatial frequency luminance stimuli can improve during smooth pursuit eye movements (Schutz, Braun, Kerzel, & Gegenfurtner,

2008). However, there may be a difference between increased sensitivity at threshold luminance stimuli reported by Schutz et al, and improvements in how well supra-threshold luminance stimuli enhance colour signals (the contour effect).

Taken together, these results suggest that afterimages during fixation and pursuit are no longer enhanced by a contour to the same extent when saccade-like jitter is added to the contour. This lends support to the possibility that contour and afterimage misalignment is driving the reduction in the contour effect in the saccade condition. However, there are a number of reasons why it is likely that the contour and afterimage misalignment stimulated in this experiment is an upper estimate of the misalignment during the saccade condition. First, we did not filter the eye movement data and this may have resulted in added jitter produced by eye tracker noise. It is difficult to address this problem because if a filter is not completely accurate we run the risk of removing some of the saccade jitter as well as the eye tracker noise. Second, because the eyes will have produced additional jitter during the fixation and pursuit conditions of this experiment, this jitter would then have been added to the saccade jitter we simulated. Third, the contour was turned off completely during periods corresponding to saccades. However, it is likely that not all visual features are suppressed during saccades (Burr, Morrone, & Ross, 1994; Uchikawa & Sato, 1995) and that features during a saccade can influence perception even if they do not reach conscious perception (Ibbotson & Cloherty, 2009).

Furthermore, it is difficult to argue that Experiment 3.4 was able to completely equate the contour condition with fixation and pursuit conditions, because even though the contour was misaligned with the afterimage, we have introduced a contour that is potentially very distracting. Thus, in order to confirm that the drop in contour enhancement in the saccade condition is due to a greater degree of contour-afterimage misalignment, we used a paradigm in Experiment 3.5 that does not introduce an attentional difference between saccade and fixation conditions and offers better equality of contour-afterimage alignment.
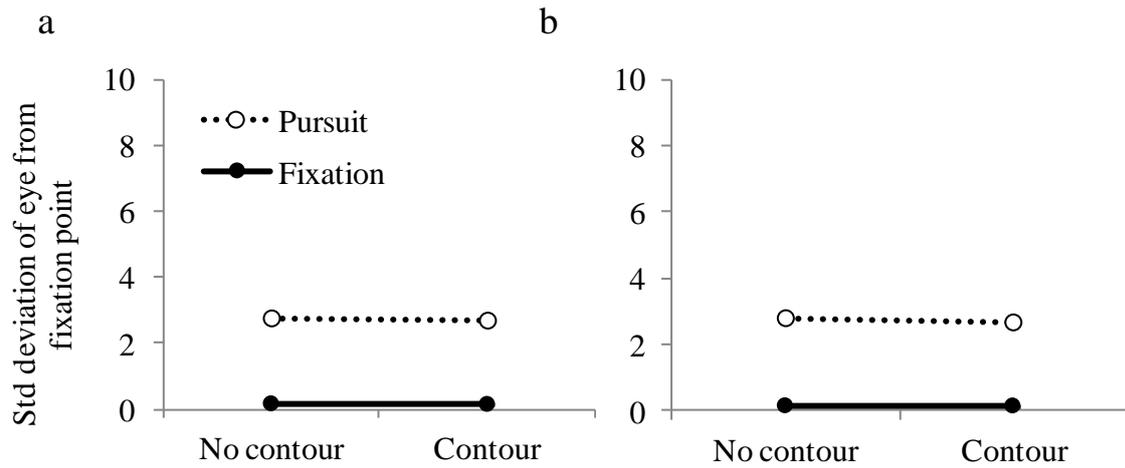
Figure. 3.6. Accuracy of gaze position from point of fixation in the large jitter (a) and small jitter (b) conditions. In both the contour and no contour conditions, gaze accuracy is much better for fixation (black lines) than pursuit (dotted lines).

Experiment 3.5: Gaze contingent contour during fixation and saccade conditions

To better equate the level of distraction and the degree of contour-afterimage misalignment between fixation and saccade conditions, we used a gaze contingent design in Experiment 3.5. Eye movements were recorded online and the contour position was continually adjusted so it remained in the centre of gaze direction. Thus, the only point at which the contour was not aligned with the afterimage in the saccade condition is during the saccade itself. We switched off the contour during these periods, and yoked these durations to insert into future fixation trials.

The advantage of this procedure is that any unequal distraction effects that may have been present in the fixation condition of Experiment 3.4, which were produced by the contour jittering around the fixation point, were now reduced. However, because the contour is now contingent on gaze direction, the alignment of the contour and the afterimage should be more equated across fixation and saccade conditions. This allows us to explore whether the reduction in the contour effect in the saccade condition of Experiment 3.1 was due to a misalignment of the contour with the afterimage. In turn, this may help to resolve why we found an opposite result to what would be predicted by our hypothesis that the contour effect increases with signal ambiguity.

As previously we have shown that fixation and pursuit conditions are similar with respective to afterimage duration with and without a contour, in Experiment 3.5 we focused on the comparison between fixation and saccades. We ran two sessions in Experiment 3.5, one with a long (3s) adaption durations to prevent the occurrence of floor effect, and one with short (1.5s) adaption durations to allow comparison with Experiment 3.1b.

Methods

Observers

Eight observers (seven naive, one author; five males, three females) participated in Experiment 3.5. All had normal colour vision and normal or corrected-to-normal visual acuity.

Apparatus

A new laboratory set-up was used in Experiment 3.5 because the gaze-contingent design required the use of an eye tracker with a higher sampling rate of 1000Hz (Eye Link 2000). Stimuli were generated by a PC running OpenGL, and presented on a 19in Viewsonic P225F monitor (100Hz refresh rate). Observers were tested in a dark laboratory, and sat at a viewing distance of 70cm with head movements stabilised using a chin rest.

Drift correction

Each observer was calibrated with the eye tracker at the beginning of the experiment. In order to insure continuous accurate gaze contingency throughout the experiment a short drift correction was conducted at the beginning of each trial. A red (x = 0.621, y = 0.34, Y = 5.6) 0.1° dot placed +/-2° from the centre of a screen was displayed for 500ms. If 95% of the eye trace samples within this period were within 0.3° of the mean gaze location, fixation was accepted. Observers were informed with a beep and a 2.5° cross on the screen when fixation was unaccepted, and were required to repeat the procedure until fixation was accepted.

Stimuli and procedure

All stages of the experiment were conducted on a homogenous grey background (x = 0.288, y = 0.303, Y = 8.5). Observer's fixated a pink (x = 0.279, y = 0.147, Y = 9) or green (x = 0.289, y = 0.609, Y = 9) 3° circle, presented 4° to left or right of centre. In the long adaptation session, observers adapted for 3s, while in the short adaptation session they adapted for 1.5s. A 0.1° black dot (x = 0.346, y = 0.301, Y = 2.7) was presented in the middle of the adaptation circle to maintain fixation, and this dot remained after the adaptation circle was turned off to begin the afterimage measurement phase. During fixation trials, the dot remained in the same screen location throughout the trial. During saccade trials, the dot jumped from 4deg to the left and right of the screen at a frequency of 1.67Hz. Observers pressed one response key when they perceived that the afterimage had completely faded and a separate response key if they had not seen an afterimage at all.

During the afterimage measurement phase, gaze location was recorded online and a grey (x = 0.289, y = 0.302, Y = 7.5) 3° contour (0.15° wide) was presented so that it was continually

centered on gaze direction (i.e. gaze contingent). Saccades were detected using a speed detector based on difference between current and previous eye tracker sample with a velocity criterion of 20°/s. During saccade trials, the contour was not presented during samples that were detected as saccades. During fixation trials, the saccade durations were yoked from the saccade trials and the contour was turned off during these intervals. This method required that the first trial for each observer was always a saccade trial. The contour was turned off during saccades and for saccade-length intervals during fixation to equate saccadic suppression of the contour between fixation and saccade conditions (i.e. by eliminating it in the saccade condition).

Despite drift correcting at the beginning of each trial, the accuracy of the calibration did occasionally slip, resulting in a small displacement of the contour from gaze direction. In order to reduce this, an algorithm was employed to carry out a continuous drift correction throughout the trial. When gaze direction was within 2° of the fixation dot we assumed that the observer was foveating the dot accurately. Therefore the difference between the sample and the fixation target was assumed to reflect an error between the gaze location and the eye-tracker output. This discrepancy was subtracted from the subsequent sample in order to try and recreate veridical gaze location.

Results and Discussion

Figure 3.7a shows an equal increase in afterimage duration by the contour in both the fixation and saccade conditions for long adaptation durations (main effect of contour $F(1, 7) = 8.37$, $p < 0.05$; eye-movement x contour interaction $p = 0.50$, *n.s.*). These results suggest that when misalignment of the contour with the afterimage is more equal across saccade and fixation conditions, the effect of the contour and saccades on afterimage duration is additive. Overall, afterimage durations were longer during fixation than during saccades (main effect of eye movement, $F(1, 7) = 11.29$, $p < 0.01$), which confirms our previous findings that afterimage duration is reduced during saccades relative to fixation. The results for the shorter adaptation session are shown in Figure 3.7b and follow a similar pattern to the long adaptation session. Due to the small percentage of trials where an afterimage was seen for some participants, the results from the short adaptation session were not statistically analysed as the mean of the durations may not be reliable.

Figure 3.7 shows the percentage of trials where an afterimage was seen for both the long (c) and short (d) adaptation sessions. For both saccade and fixation conditions, the contour significantly increased the likelihood of perceiving an afterimage (main effect of contour: long adaptation, $F(1, 7) = 19.18$, $p < 0.01$; short adaptation, $F(1, 7) = 51.51$, $p < 0.001$). Despite finding an increase in afterimage duration during fixation relative to saccades, fixation did not significantly increase the percentage of trials where an afterimage was seen, relative to saccades (main effect of eye movement: long adaptation, $p = 0.31$, n.s.; short adaptation, $p = 0.96$, n.s.).

However, the contour did increase the likelihood of perceiving an afterimage at all more in the saccade condition than in the fixation condition (eye movement x contour interaction: long adaptation, $F(1, 7) = 11.3$, $p < 0.01$; short adaptation, $F(1, 7) = 6.56$, $p < 0.05$). This interaction suggests that the contour cue may dominate over the saccade cue in the initial decision of whether to perceive the afterimage.

In summary, the interaction we observed in the earlier Experiment 3.1b where a smaller effect of the contour was found in the saccade condition than in the fixation or pursuit conditions appears to disappear when contour and afterimage alignment is better equated across eye movement conditions. The overall consensus from Experiment 3.4 and 5 is that the effect of the contour and the saccades on afterimage duration are additive. The contour will increase afterimage duration, while concurrently, the saccades will reduce it. However, the finding that the contour increases the percentage of trials where an afterimage is seen more in the saccade condition than the fixation condition, suggests that the contour cue may dominate the perceptual decision of whether to perceive the afterimage in the first instant more than the saccade cue.
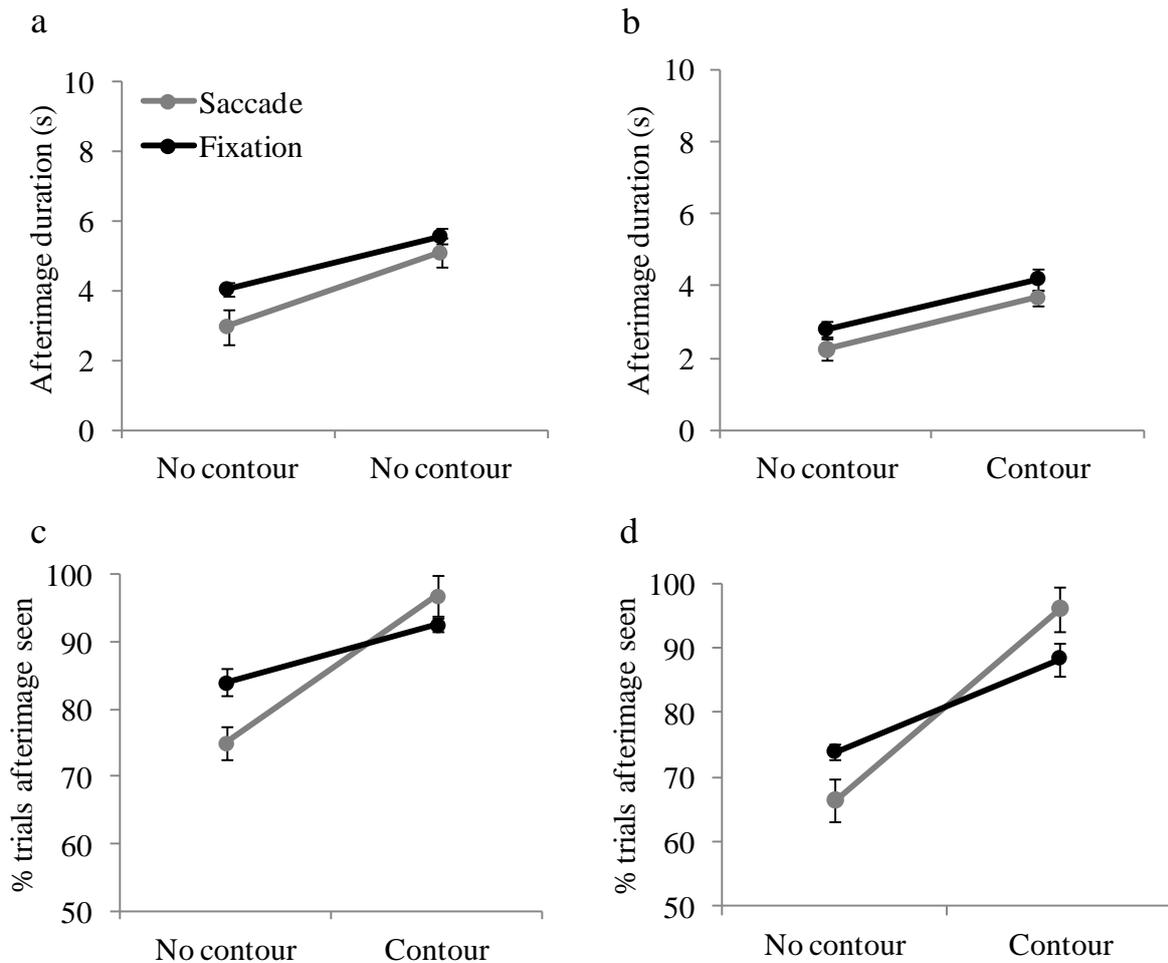
Figure 3.7. Results from Experiment 3.5. Long adaption (3s) shown in a-b, short adaptation (1.5s) shown in c-d. (a) For long adaptation durations, afterimage duration is increased equally by the contour in both fixation (black) and saccade (grey) conditions. (b) A similar pattern of results is seen in the short adaptation condition as the long adaptation condition: the effect of the contour is additive for the fixation and saccade conditions. (c) The percentage of trials where an afterimage is seen is increased by the contour in relatively more in the saccade than the fixation conditions. (d) The pattern shown in (c) is similar in the short adaptation condition: the contour increases the percentage of afterimages seen trials more in the saccade than fixation condition.

Chapter 3 Discussion

After exploring how luminance edges enhance afterimages in Chapter 2, we were interested in other cues that might modulate our perception of afterimages, particularly those that act in the opposite way and diminish afterimage perception. There are many historical reports that saccadic eye-movements reduce, or change, afterimage perception (Darwin & Darwin, 1786; Ferree, 1908; Fiorentini & Mazzantini, 1965; A. H. Friedman & Marchese, 1978; Helmholtz, 1962; Kennard et al., 1970; Yarbus, 1967). The experiments in this chapter aimed to confirm these reports and test the various suggested explanations for this effect. We also investigated two predications for how luminance edge cues and different eye movements would interact in their modulation of afterimage perception (shown in Figure 3.1). Contextual cues or saccade cues could be combined in an additive way and both influence afterimage perception. Alternatively, either context or saccades could dominate the perceptual interpretation of the afterimage signal.

Afterimage duration is reduced by saccades relative to fixation, pursuit and blinks

When we originally explored the effect of saccadic eye movements on afterimages in Experiment 3.1, we found no significant difference in afterimage duration (with no contour present) between saccade, pursuit and fixation conditions. However, after adjusting for floor effects in the adaptation duration in Experiment 3.2a, we then observed that saccades significantly reduced afterimage duration. This reduction increased with the frequency of the saccades. These results are consistent with previous experiments reporting a reduction in afterimage duration following saccadic eye movements (Fiorentini & Mazzantini, 1965; Kennard et al., 1970). Saccades also significantly decreased the likelihood that the afterimage was perceived at all, although this effect did not significantly increase with saccade frequency.

Smooth pursuit eye movements did not significantly reduce afterimage duration relative to fixation, although there was a slight trend for durations to be lower during pursuit than fixation (Experiment 3.2b). This trend was not present in the percentage of trials where an afterimage was seen, which this was equal across fixation and pursuit. Our findings are therefore consistent with the few authors who have explored the effect of pursuit on afterimage perception (Darwin & Darwin, 1786; Fiorentini & Mazzantini, 1965). Comparison

of the difference between afterimage durations during saccades and during pursuit (after normalising on their respective fixation baselines) revealed that durations during saccades were reduced significantly more than during pursuit.

Repetitive blinking at the same frequency as saccadic eye movements did not reduce afterimage duration or decrease the likelihood that the afterimage was seen at all (Experiment 3.3). This result challenges the suggestion that blinks will cause an afterimage to disappear (Helmholtz, 1962; Kennard et al., 1970). Taken together, these results suggest that saccadic eye movements have a specific ability to reduce afterimage duration and decrease the probability of perceiving an afterimage at all.

Why do saccades influence afterimage perception

In the introduction to this Chapter we discussed four main theories for why saccades reduce afterimage perception. First, saccadic eye movements produce changes to the retinal image, including shifting background contours (Chapter 2), variations in luminance (Helmholtz, 1962) and smearing (Hering, 1891, as cited in, Ferree, 1908). Second, contractions of the extraocular muscles during eye movements may alter the vascular state of the retina, which in turn may relive adaptation (Flick and Gurber cited by Exner, 1890; Matin, 1974). Third, real stimuli are suppressed around the time of the saccades ('saccadic suppression') and afterimages may be suppressed by similar mechanisms. Fourth, saccadic eye movements could decrease the likelihood that the afterimages signal represents a real object, because real objects do not remain fixed at the same retinal location across saccadic movements (Coren & Porac, 1974; Exner, 1890; Fiorentini & Mazzantini, 1965). Table 3.1 shows a summary of the four main theories and the evidence for and against them, pooled from previous research and the experiments reported in this chapter.

1. Retinal image changes – context, illumination
In Chapter 2 we showed that context is a powerful modulator of afterimage perception. It is unable to explain the results reported in this chapter, however, because the experiments were conducted on a homogenous background. This means that there was no change in background contours or illumination across saccades. We also found that blinks do not reduce afterimage duration, despite producing changes in retinal luminance (Experiment 3.3). Thus, context

changes to the background may affect afterimage duration, but are not the only explanations for the effect of saccades on afterimages. Changes in retinal luminance can influence afterimage perception; they can flip their polarity from positive to negative (Darwin & Darwin, 1786; Matteson, 1965; Robertson & Fry, 1937), and in some cases even prolong their duration (Gerling & Spillmann, 1987; Magnussen & Torjussen, 1974; Matteson, 1965; Robertson & Fry, 1937). However, our findings suggest that they do not significantly reduce afterimage duration.

2. Changes to physiological state of retina

The largest challenge to theories suggesting that saccades produce changes to physiological state on the retina is that these theories may not be viable with our current understanding of retinal processes. Through reviewing the current literature, it has been difficult to establish whether movements of the extraocular muscles produce significant changes to the vascular state of the retina. Blinks and saccades do increase IOP, but not enough to affect retinal blood flow (Flynn, 2003; Kaufman et al., 2003). Furthermore, it is unclear whether changes to the vascular state on the retina could relieve adaptation of photoreceptors or retinal ganglion cells.

However, even if there is some truth in the mechanisms underlying these theories, they do not suggest exactly what type of muscle contraction is required to change the vascular state of the retina and produce afterimage suppression. Blinks, saccades, fixation and smooth pursuit eye movements all produce contractions of the extraocular muscles. These muscles are composed of various fibre types, which probably all contribute to generating the full spectrum of eye movements (Evinger et al., 1984; Leigh & Zee, 1999; Scott & Collins, 1973). Rapid eye movements may utilise the global, less fatigue-resistant fibers, whereas maintaining a steady gaze may rely more on orbital fatigue- resistant fibres (Leigh & Zee, 1999). Thus, it is possible that saccades may produce slightly different contractions to pursuit and fixation. Blinks are possibly most similar to saccades in terms of the similarly in extraocular muscle contractions. For example, blinking can facilitate saccade speed in clinical disorders such as Huntington's disease and posterior fossa abnormalities (Leigh et al., 1983; Zee et al., 1983). In our experiments we found no consistent evidence that blinks or pursuit eye movements significantly decrease afterimage duration or influence that likelihood that an afterimage is seen at all. Thus, if these theories are to be accepted, then it would have to be assumed that the only muscle contractions that relieve adaptation on the retina are those that generate

saccades. Perhaps more importantly, these theories unable to explain why entopic images are suppressed more quickly during saccadic eye movements (Coren & Porac, 1974), as in these cases there is no adaptation state on the retina to relieved.

3. Saccadic suppression

It is unlikely that classic saccadic suppression mechanisms can account entirely for the effect of saccades of afterimage perception. Firstly, because the duration of afterimage disappearance following a saccade is longer than the transient decrease in sensitivity observed for real stimuli. Secondly, because it cannot explain why overall afterimage duration is reduced following multiple saccades. Saccadic suppression mechanism could explain previous reports that afterimages are continually suppressed during continual, fast saccades (Kennard et al., 1970). However, because saccadic suppression only lasts for around 50-100ms around the time of the saccades, the saccade frequency would have to be very fast to trap the afterimage within a loop of saccadic suppression. We have shown that during fast frequency saccades at 3.37Hz afterimages are often still visible initially (Experiment 3.2a).

Furthermore, we have reported that afterimage duration, and the likelihood of a perceiving an afterimage, is not reduced during continual blinking (Experiment 3.3). This result is difficult to explain with saccadic suppression theories as blink suppression of real stimuli is similar in time course and magnitude to saccadic suppression of real stimuli (Burr, 2005; Ridder III & Tomlinson, 1993, 1997; Volkmann et al., 1982). Saccadic suppression is also unable to explain why entopic images are suppressed more quickly during saccadic eye movements than during fixation (Coren & Porac, 1974). Finally, magnocellular signals representing low spatial frequency luminance stimuli are most likely to be suppressed during a saccade, while parvocellular signals, representing colour stimuli, remain relatively unaffected (Burr et al., 1994). Thus, saccadic suppression mechanisms would be unable to explain the results of the present experiments where colour afterimages were used.

4. Exner's theory – likelihood afterimage signal represents a real object

The final explanation for why saccades reduce afterimage perception is that they act as a cue to the visual system that the afterimage is not a real object. This theory was first developed by Exner (1890), who argued that because afterimages move with the edges during a saccade in a way that is unlike real objects (which would change retinal location but not spatial location), the visual system will suppress the afterimage. A similar theory was suggested by

Coren and Porac (1974) after they observed that stabilised images disappear more quickly during saccadic eye movements than fixation. They proposed that saccades produce a decorrelation between eye movement signals and the retinal image. These theories are essentially using different language to describe the same effect - the original correlation between efferent signals and the retinal image will have been developed through knowledge of how objects in the world move relative to eye position. This theory fits well with the framework developed throughout this thesis: afterimage signals are inherently ambiguous, which produces a degree of perceptual uncertainty over whether to perceive them. Saccadic eye movements will decrease the likelihood that the afterimage represents a real object, leading to a reduction in afterimage duration and a decrease the probability an afterimage is perceived at all.

This theory is able to explain why afterimages are suppressed when viewed in the dark or against a uniform background. All that is needed is the eye movement signal to reveal that the afterimage acts unlike a real stimulus, rather than relying on associated changes to the background context, such as contour shifting or variations in illumination and smearing.

The experiments presented in this Chapter offer further support for this theory. Saccadic eye movements reduce afterimage perception relative to fixation. While pursuit eye movements and blinking, which do not force the afterimage to move in a way that is unlike a real stimulus, do not result in a reduction in afterimage duration. We also found that saccadic eye movements also reduced the likelihood that an afterimage was seen at all. During these trials, it is possible that the afterimages were relatively weaker and so were suppressed immediately following the first saccade. We have speculated that weak afterimages signals, which are highly ambiguous to the cortex, will be suppressed quickly following a saccade. While strong afterimage signals may require multiple saccades before the evidence that they are purely retinotopic outweighs the strong signals sent from the retina.

We have taken the finding that afterimage duration during pursuit is not reduced relative to fixation as support for the theory that pursuit eye movements do not distinguish an afterimage percept from a real object. However, previous studies have reported that visual sensitivity for flashed real stimuli is improved during smooth pursuit eye movements relative to fixation (Schutz et al., 2008). The explanation for this finding is that feedback processes boost the

parvocellular pathway during pursuit to compensate for motion blur produced by the eye movement. However, because the stimuli in Schutz et al's (2008) study were flashed targets, whereas in our experiment the afterimages were perceived for several seconds, we cannot be sure of the extent to which Schutz et al's findings can be generalised to our results.

	Retinal image changes - context, illumination	Retina changes - extraocular muscle contraction	Saccadic suppression	Exner's theory
Afterimage duration decreased by saccade	✓	✓	✗	✓
Disappear after saccade then return	✗	✗	✗	✓
Suppression/disappearance longer for afterimages than real stimuli	✓	✓	✗	✓
Saccade effects occur in dark	✗	✓	✓	✓
Saccade effects occur on homogenous backgrounds	✗	✓	✓	✓
Blinks do not suppress afterimages	✗ - illumination ✓ - context	–	✗	✓
Consistent with current understanding of visual system	✗ - illumination ✓ - context	✗	✓	✓
Entopic images suppressed by saccades	✓	✗	✗	✓
Afterimages not suppressed during pursuit	✓	–	✓	✓
Fast saccades – afterimages do not return during fixation	✗	✓	✓	✓

Table 3.1. List of reported eye movement and blink effects on afterimage perception, compared against the four possible explanations for the effect of saccades. If a theory can explain, or is compatible with, a particular effect it is marked with a '✓', a '✗' if it cannot explain, or is not compatible with, the effect and a '–' if it we cannot tell if it can explain, or is compatible with, the effect.

Physiological mechanisms behind Exner's theory

The theory that afterimages are suppressed following a saccade because they behave unlike a real object is a higher level interpretation of how the brain processes afterimage signals. It is possible to speculate about a number of physiological processes that could contribute to the lower level description of this theory. As previously noted, the explanation relies on the well established existence of cortical efferent signals about impending voluntary eye movements. Only voluntary eye movements produce afterimage disappearance; pressing the eyeball to produce involuntary movement does not suppress afterimages (Bell, 1823; Ferree, 1908).

One possible explanation is mechanisms that relate to trans-saccadic integration and remapping. It has been found that attention is shifted to a post saccadic location before a saccade and this produces re-mapping of receptive fields (Merriam, Genovese, & Colby, 2007; Nakamura & Colby, 2002). This remapping allows receptive fields at post saccadic locations to shrink and shift towards the saccade target, improving visual sensitivity (Tolias et al., 2001). These processes are likely to explain findings that the perceived hue of a stimulus presented in a future fixation position biases the perceived hue of a stimulus presented postsaccadically at the same spatial, but different retinal, location (Wittenberg, Bremmer, & Wachtler, 2008). When the predicted hue of a post saccadic location differs widely from the perceived hue after the saccade (due to the presence of an afterimage) the brain may attempt to compensate for the discrepancy to maintain perceptual stability. Thus, in our experiments, the visual system has knowledge that the post saccadic location is not the same hue as the afterimage, which could produce bias in afterimage perception towards the background. As our backgrounds were grey, this would translate to a decrease in afterimage saturation.

Pre-saccadic re-mapping of receptive fields implies that associations are formed between eye movement signals and responses of visual neurons. These associations may embody how the visual system learns to anticipate the visual response to objects in the world as the eyes move around it. This not only enables the world to remain stable on the retina, but also for the visual system to distinguish what is in the world and what is only on the retina. A possible assumption that is learnt about the world is that it remains stable most of the time. Therefore, if a patch on the visual field changes hue across a saccade (e.g. when it is viewed first in the

periphery and then in the fovea) it is likely that this hue change is due to artifact of the retina and not an object in the world. This is exactly the situation that is produced by afterimages and other stabilised images across saccadic eye movements.

Contour and eye movement interactions

The second aim of this chapter was to explore how different cues that influence the likelihood of perceiving an afterimage signal interact with one another. In Chapter 2 we concluded luminance contours increase the likelihood that an ambiguous afterimages signal represents a real object. In this Chapter we have argued that saccades act in an opposite way to luminance contours and decrease the likelihood that the afterimage signal represents a real object. We were interested in whether these two cues would be combined additively, or whether one cue would dominate the other and influence afterimage perception to a greater extent. Initial results from Experiment 3.1 suggested that the saccade dominated the afterimage perception, as less contour enhancement was found for afterimages during saccades than during pursuit or fixation. However, further exploration of this result revealed that the when contour-afterimage alignment was equated across eye movement conditions, the contour increased afterimage duration relatively equally across fixation and saccade conditions (Experiment 3.4 & 5). This suggests that there is a combined influence of the luminance contour and the saccade cue on afterimage duration. Interestingly, the contour increased the percentage of trials where an afterimage was seen at all more in the saccade than fixation condition. A possible explanation for this is that the contour dominates perception in the first instant, or the initial decision of whether to perceive the afterimage at all, and after this both cues are combined. Overall, context appears to be a stronger cue than saccadic eye movements, perhaps because the afterimages were fairly short in duration and the effect of saccades increases with a larger number of saccades.

Limitations of Experiment 3.4 & 3.5

The aim of both Experiment 3.4 and 3.5 was to equate the alignment of the contour with the afterimage across fixation, pursuit and saccade conditions. In Experiment 3.4, we inserted extra contour misalignment into the fixation and pursuit conditions to mimic misalignment during saccade trials. In Experiment 3.5 we made the contour gaze-contingent so that it

remained around the afterimage even when observers' eyes moved from the fixation dot. As previously discussed, the limitation of Experiment 3.4 is that the contour misalignment may have been over estimated. The limitation of the gaze contingent design in Experiment 3.5 is that the contour could become more ambiguous because it too now moves in a way that is unlike a real object. This interpretation seems unlikely because we observed a strong contour effect for both saccades and fixation and may be more of a concern if the eye tracking apparatus allowed for better image stabilization. However, this in itself means that the misalignment may have been under estimated in the saccade condition. Perfect stabilisation is almost impossible, even with a Purjinke eye-tracker, thus it would be difficult to overcome this limitation. The other possibility is that the gaze-contingent contour, that produces strong retinal signals, encourages the brain to learn that real objects can move with the eyes. Learning of this nature may decrease the ability of saccades to disambiguate afterimage signals.

Summary

The experiments in this Chapter explored the influence of different types of eye movements and blinking on afterimage duration and investigated how eye movement cues interact with contextual edges to influence afterimage perception. Our results suggested that saccadic eye movements reduce afterimage duration and decrease the likelihood of perceiving an afterimage relative to blinking, pursuit or fixation. We also found that luminance edges and saccadic eye movements are combined additively in their influence on afterimage duration, so that luminance edges increase duration while saccadic eye movements concurrently decrease it. However, luminance edges may dominate perception in the first instance as they increase the likelihood of perceiving an afterimage at all relatively more than saccades decrease this likelihood. We discussed four different theories of why saccadic eye movements diminish afterimage perception and argued that our results are consistent with the interpretation that saccades cause an afterimage to move unlike a real object, thus leading to their suppression.

Chapter 4: Colour distortions across the visual field

Introduction

In Chapters 2-3 we examined how our perception of afterimages is influenced by the conditions they are viewed under, and suggested that this could explain why we rarely perceive them in real world viewing. In this Chapter we focus on retinal colour distortions across the visual field, which are produced mainly by the presence of macular pigment in the fovea which preferentially filters short wavelength light (Bone et al., 1992; Chen et al., 2001). Like afterimages, these distortions are produced on the retina and do not represent meaningful properties of the word. Also, they are not normally noticed in everyday viewing, but they can be perceived in controlled laboratory conditions (e.g. Abramov et al., 1991; Hansen et al., 2009; Parry et al., 2006; Webster et al., 2010).

It is somewhat more surprising that these colour distortions are perceived under some conditions than it is that for afterimages. This is because macular pigment remains fairly constant in the adult retina, allowing ample time for the distortions to be calibrated away. Further, as discussed in the General Introduction, research from our lab has shown that the chromaticity shifts between the fovea and periphery are predicable enough to generalise to new surfaces (Bompas et al., 2013). As long as such generalisability exists, any theory in which perceived colour is calibrated continually throughout the lifetime would predict that sampling the same surfaces at different eye positions would result in colour stability across the retina.

One possibly for why these colour distortions remain is that they are perceived in unnatural laboratory conditions but not when conditions are more similar to natural viewing. Specifically, we hypothesise that compensatory mechanisms may exist for natural viewing conditions because these are the conditions that the visual system has learnt over the time to perceive. In this Chapter, we measured colour distortions under two conditions that are more similar to everyday viewing. First, we used stimuli composed of natural spectra instead of computer-generated spectra (Experiment 4.1). Second, we explored a more natural condition where the surface remains in the same spatial position but the eyes move to produce a

difference in retinal position of the surface instead of the more typical opposite presentation (Experiment 4.2).

Experiment 4.1: Retinal hue variations with natural stimuli

Until recently, all of the studies reporting colour differences across the retina had used computer-generated stimuli. However, most of the learning and calibration the visual system carries out across the lifetime, and over evolutionary history, is in response to natural not computer-generated spectra. There is always the risk that perceptual differences found for computer-generated stimuli will not generalise to natural surfaces under natural illuminates. Natural spectra are smoother across wavelengths than computer-generated spectra. CRT monitors rely on combined ratios from the three RBG guns, leading to three wavelengths corresponding to these guns dominating the spectra.

It is possible for natural and computer-generated stimuli to be metamers and appear perceptually identical if they produce the same relative activation of LMS cones. However, macular pigment filtering will affect natural and computer spectra differently because the spectra themselves are very different.   Thus, just because a computer-generated spectrum and a natural spectrum produce identical colours in the fovea, does not mean that the two spectra will still produce identical ratios of LMS activation in the periphery after macular pigment filtering (see Figure 4.1 for graphed illustration of this).

In Experiment 4.1, we tested whether colour distortions across the visual field were still present with two types of natural surfaces, viewed under natural daylight. Fruit juices (cranberry & purple grape) were mixed to obtain perceptually continuous hues (Exp. 4.1a) and we also used natural pigmented papers from the Farnsworth and Munsell 100 Hue test (Exp. 4.1b; Farnsworth, 1943; Nickerson & Granville, 1940).   The Farnsworth-Munsell papers are preferable to the fruit stimuli because they have a long history of development, testing and standardisation. Further, because the hue increments are roughly equivalent and based on just noticeable differences (JNDs) it enables us to quantify any hue-shifts better.

Stimuli were selected from the purple range because the largest perceptual differences should occur when stimuli contain both short and long wavelengths (e.g.Murray et al., 2006). In both

Experiment 4.1a and 4.1b, observers were required to judge if a constant foveal stimulus was 'pinker' or 'bluer' than a varying peripheral patch (constant stimulus design). We then calculated the PSE in colour space, or the peripheral stimulus hue that perceptually matched the constant foveal hue. The retinal hue variation that is expected due to macular pigment is that the PSE is shifted towards pinker hues to compensate for more bluish light reaching peripheral cells. However, if retinal hue variations are reduced when natural stimuli are used we predicted that the PSE will be closer to the physical point of equality.

Since conducting these experiments, Parry, Panorgias, McKeefry and Murray (2012) have reported that colour distortions are still present for natural stimuli between the fovea and a retinal eccentricity of 18deg. However, in our experiments we examined colour differences between the fovea and near periphery (less than 3°) and tested two types of natural stimuli. Our motivation for testing in the near periphery is that this area used more frequently for colour-driven tasks than the far periphery, and thus is more likely to be subject to learning effects.
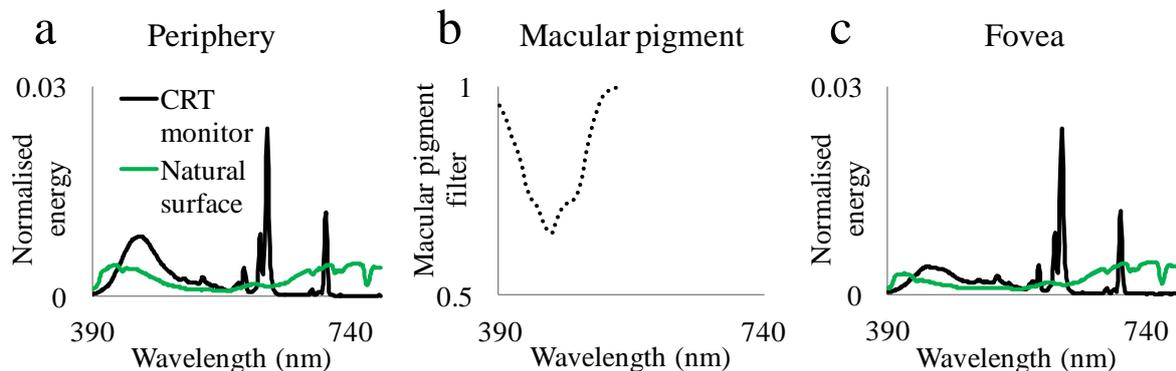
Figure. 4.1. Natural and computer-generated spectra in the fovea and periphery. *(a)* CRT monitor (black line) and natural surface (green line) spectra lead to the perception of an identical colour (i.e. are metamers) in the periphery. *(b)* Macular pigment filter absorption is largest for short-wavelengths. *(c)* The same computer and natural spectra in the fovea, but after macular pigment filtering. The two spectra have been affected differently by the macular pigment filter and so the resultant percepts will no longer be identical in colour.

Methods

Observers

Four naive observers (two males, two females) participated in Experiment 4.1a and five observers (two males, three females; no authors) participated in Experiment 4.1b. All subjects had normal colour vision and normal or corrected-to-normal acuity.

Apparatus and Stimuli

Each stimulus was measured with a spectroradiometer (CRS SpectroCAL) and MacLeod & Boynton (MCB, 1979) chromaticity coordinates were calculated for each spectrum and are shown in Figure 4.2b. The average luminance was around 200cd/m^2, but varied from day to day depending on natural daylight levels.

Experiment 4.1a

The stimuli were seven 20ml clear cylinder Perspex pots filled with differing ratios of purple grape and cranberry juice to produce a perceptually continuous range of purple hues. Milk was added to equate luminance levels. The foveal stimulus remained a constant chromaticity throughout the experiment and there were seven variations in chromaticity of the peripheral stimuli which were centred around the foveal pot chromaticity. See Figure 4.2a for a photo of the fruit juice stimuli. The stimuli were presented to observers at eye level against a grey background, and were positioned 2.78° to the left and right of straight ahead at a viewing distance of 72cm. A grey card was manually lifted to expose the stimuli. Observers were required to fixate a 0.29° black dot on the background card, positioned in front of either the left or right pot.

Experiment 4.1b

Stimuli were selected from the Farnsworth Munsell 100 Hue Test and comprised isoluminant coloured pigments on matt paper mounted in black plastic caps (Farnsworth, 1943, 1949). Incremental hue variations between the caps are based on JNDs. The diameter of the caps was 2.93°, with a coloured surface of 1.86° in diameter. The blue to pink range of the Farnsworth Munsell 100 Hue Test was selected (cap no. 70 to 78). There were eight peripheral stimuli and no one peripheral stimulus was physically equal to the foveal stimulus

(four peripheral stimuli were pinker and four were bluer than the foveal stimulus). See Figure 4.2a for a photo of the caps.

The stimuli were presented in circular apertures cut from a uniform grey wooden frame (76°x88°). The stimuli were positioned 2.78° to the left and right of straight ahead at a viewing distance of 39cm. A grey 16°x6°cm screen was lifted on a manual pulley system to reveal the stimuli. Two 0.29° black dots were positioned in front of the apertures on the screen to guide fixation, and observers were instructed at the beginning of each trial which dot to fixate. See Figure 4.2c for a photo of the wooden frame apparatus.

2AFC Constant stimulus hue-matching task and procedure

For each trial in Experiment 4.1, the foveal and peripheral stimuli were displayed simultaneously for approximately 1000ms, and the observers were required to verbally state if the foveal stimulus was 'pinker' or 'bluer' than the peripheral stimulus. The foveal cap remained a constant chromaticity and the hue of the peripheral cap was varied. Participants were instructed to fixate (binocularly) on the black dot, positioned in front of either the left/right pot dependent on trial. Gaze direction was monitored by the experimenter, and trials in which fixation was not accurate were repeated at the end of the trial block.

In Experiment 4.1a, observers received a total of 70 trials; 10 repetitions of each peripheral patch chromaticity. For experiment 4.1b, observers received a total of 80 trials; 10 repetitions of each peripheral patch chromaticity. For both experiments, the position of the foveal patch (left/right) was counterbalanced. The observers were tested a laboratory illuminated with natural daylight from a large northeast facing window (295cm x 141cm), behind the observer's seat (Figure 4.2d). Psychometric functions were fitted for each observer and the PSE was extracted.
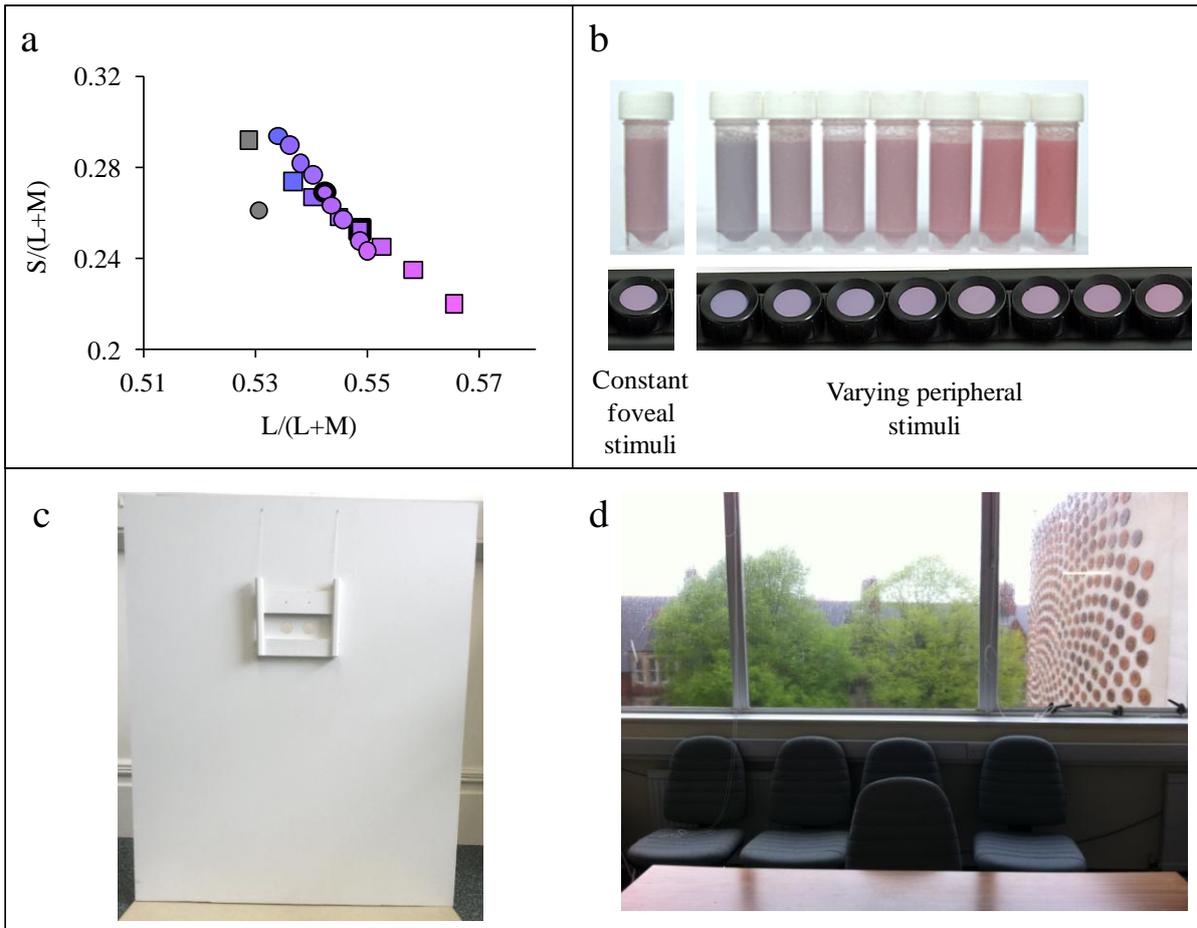
Figure 4.2. Stimuli used in Experiment 4.1. *(a)* MacLeod & Boynton (MCB, 1979) chromaticity coordinates chromaticity coordinates for the fruit juices (squares) and Farnsworth-Munsell 100 Hue papers (circles) and their respective grey backgrounds. Black outline denotes the constant foveal stimulus. *(b)* Fruit juices from Exp 4.1a (top) and Farnsworth-Munsell papers from Exp 4.1b (bottom). Offset on the left is the foveal stimulus used in both experiments, and to the right are the varying comparison peripheral stimuli. *(c)* Apparatus used in Experiment 4.1b to display the Farnsworth-Munsell papers and *(d)* the laboratory with a large window providing natural daylight.

Results and Discussion

Figure 4.3 shows psychometric functions for all observers in Experiment 4.1a (fruit juices, *a*) and Experiment 4.1b (Farnsworth-Munsell papers, *b*). One sample t-tests revealed that the point of subjective equality (red diamond) is significantly shifted towards pink for both types of natural stimuli (fruit juices: $t(3)=3.74$, $p < 0.05$; FM papers: $t(5) = 5.7$, $p < 0.01$). This means that the peripheral stimuli had to be physically pinker than the foveal stimuli for them to perceptually match. This pattern is found for all observers, but one in Experiment 4.1b,

who did not display a shift. Differences across observers may be reflective of natural variation in macular pigment density, which is determined by environmental factors such as diet (Hammond et al., 1997; Sommerburg, Keunen, Bird, & van Kuijk, 1998).

In Experiment 4.2, observers were not presented an exact chip that matched the central target because we only had access to one set of FM chips. In the four observers who display step functions, this could mean that the hue-shifts were overestimated by half a JND. However, the hue differences must still have been present otherwise observers would have chosen the chip on the other side of central target 50% of the time.

The degree of shift for the Farnsworth-Munsell is small (around 0.5-1 JND) but is consistent across observers. These results confirm that retinal colour variations are still observed when viewing natural surfaces. This suggests that the question of why we do not perceive these variations during natural viewing is unlikely to be answered by a compensatory mechanism specific to natural spectra.
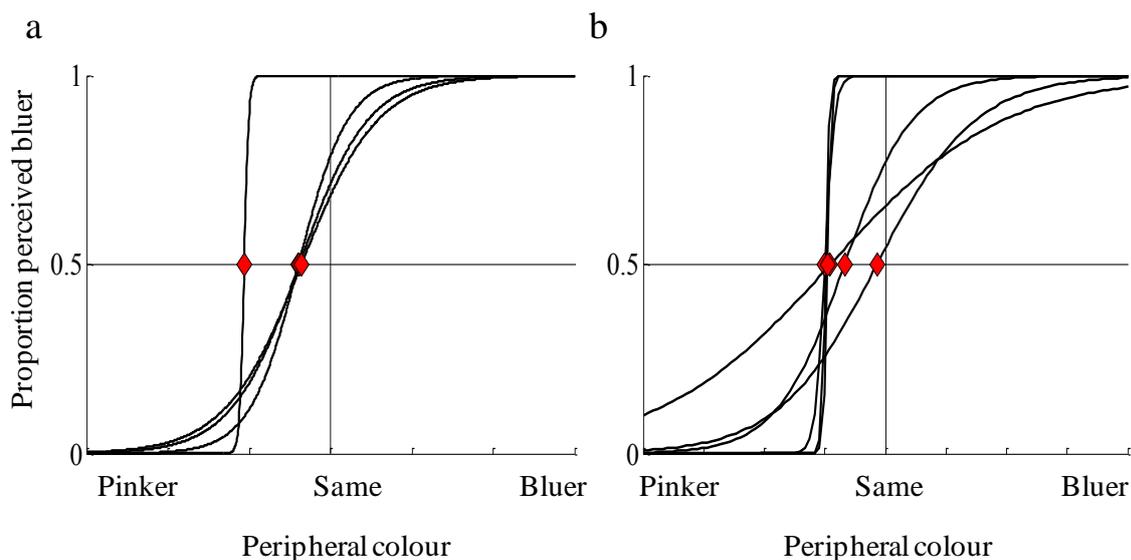
Figure 4.3. Results of Experiment 4.1, showing fovea-periphery hue shifts for two types of natural surfaces: fruit juices (a) and Farnsworth Munsell papers (b). (a) Psychometric functions for four observers in Exp. 4.1a. The variations in peripheral fruit juices are denoted by the ticks along the x-axis, from physically pinker than the foveal stimulus to physically bluer than the foveal stimulus. The proportion of responses that each peripheral stimulus was perceived bluer than the foveal stimulus is shown on the y-axis. The PSEs, where the physical stimulus is perceived as the same hue as the foveal stimulus, are denoted by the red diamonds (i.e. 50% responses bluer/pinker). For all observers, the PSE is shifted towards pink physical values, which means that a peripheral fruit juice needs to be physically pinker than a foveal fruit juice for them to perceptually match. This is consistent with the varying density of macular pigment filtering short

wavelength (bluish) light at the fovea but not the periphery (b) Similar PSE shifts are found for five out of six observers in Exp 4.1b (Farnsworth-Munsell papers).

Experiment 4.2: Colour distortions during eye movements

During everyday vision our eyes constantly perform small saccades between successive fixations (Ross, Morrone, Goldberg, & Burr, 2001), while objects in the world tend to remain stable. Because of this, the visual system has developed mechanisms to integrate oculomotor information with retinal signals to produce perceptual stability of the world across eye movements (Freeman, 2007; Ross & Ma-Wyatt, 2004). It is known that the post-saccadic appearance of a surface can be altered by information presented prior to a saccade (Melcher, 2007; Wittenberg et al., 2008). This suggests the presence of active mechanisms that maintain perceptual stability across eye movements. The sensorimotor theory of perception takes this principle a step further by suggesting that contingencies between eye position and visual stimulation are the basis of perceptual content (O'Regan & Noe, 2001). For colour vision, the prediction of this theory is that "the visual experience of a red color patch depends on the structure of the changes in sensory input that occur when you move your eyes around relative to the patch" (O'Regan & Noe, 2001, p. 951).

However, previous studies that have explored fovea-periphery hue differences have employed designs in which the eyes remain fixated and the comparison coloured patches are presented at different retinotopic *and* spatiotopic locations. Thus, it is possible that parallel mechanisms exist that compensate for the retinal colour distortions that occur when eye movement shift the retinal location of stable surfaces. In Experiment 4.2 we investigated whether hue distortions were still observed when the spatiotopic location of the coloured surface remained constant and the eyes moved (Eye movement condition), compared to a situation where the eyes remained stable, but the spatiotopic location of the coloured surface moved (Eye stationary condition).

A similar constant stimulus design to Experiment 4.1 was used in Experiment 4.2. However, in this Experiment, stimuli were displayed on a CRT monitor in order to precisely control stimulus presentation timing relative to the eye movement instructions. Also, the foveal and peripheral stimuli were presented sequentially and the foveal stimuli were varied across trials while the peripheral stimulus remained constant. The task of comparing the foveal and peripheral hues to measure the PSE remained the same, however, we were now interested in whether the foveal stimulus had to be physically bluer than the peripheral stimulus to perceptually match. This sequence is more natural as it is more common to look towards a stimulus of interest than away from it. In the Eye Stationary condition, observers gaze

remained stable throughout the trial and the location of the coloured patch moved from the periphery to the fovea (Figure 4.4a-b). In the Eye Movement condition observers performed a single, horizontal saccade between the presentation of a foveal and peripheral coloured patch, but these patches were presented in the same spatial location (Figure 4.4c-d).

If an active sensorimotor mechanism exists that reduces perceived hue differences between the fovea and periphery, we would predict that PSE would be close to the physical point of equality in the Eye movement condition. While, we would expect to observe a shift towards a bluer physical stimulus in the fovea to perceptually match the peripheral stimulus in the Eyes Stationary condition, representing the presence of no compensatory mechanism.
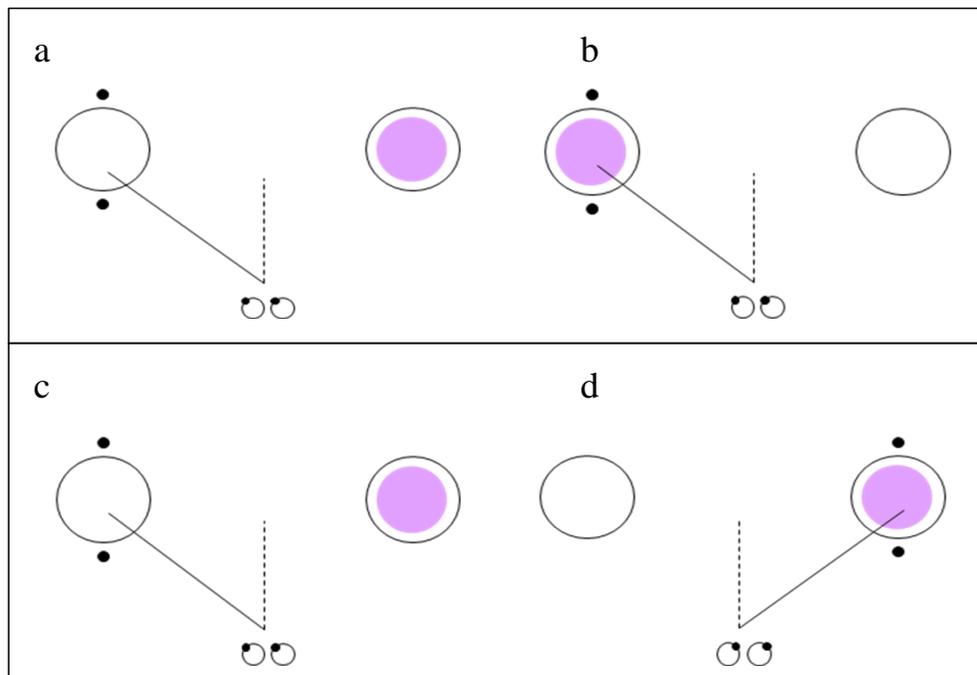
Figure 4.4. Stimulus presentation in Experiment 4.2. *Eyes Stationary condition (a)* Observers fixate the left (right) side of the screen as directed by the fixation guide dots above and below one of the two frames. The peripheral stimulus is then presented on the right (left). *(b)* Observers remained fixated on the left (right) side of the screen, and the foveal stimulus is presented on the left (right) – different retinotopic and spatiotopic locations. *Eye Movement condition (c)* Observers fixate again on the left (right) as directed, and the peripheral stimulus is presented on the right (left) *(d)* Observers make a saccade to follow the fixation dots as they move to right (left). The foveal stimulus is then presented on the right (left) – different retinotopic but the same spatiotopic location.

Methods

Observers

Seven observers (six naive, one author; two males, five females) participated in both the Eye Movement and Eyes Stationary conditions. All had normal colour vision and normal or corrected-to-normal acuity.

Apparatus and Stimuli

Apparatus is as described in Chapter 2. The stimuli were 1.86° wide circular, isoluminant coloured patches presented on a uniform grey background. The luminance of the background and patches was maintained at 34 cd/m². A black 2.17° wide circular frame (line width was 0.06°) surrounded the patches and a black 0.06° dot was positioned 0.31° above and below the foveal patch to guide fixation. The patches were positioned on the horizontal meridian, 2.78° to the left and right of screen centre.

The chromaticity of the peripheral stimulus remained constant throughout the experiment, while the foveal stimulus changes hue across trials (Figure 4.5 shows chromaticity coordinates for Session 1). There were nine hues of the foveal stimuli and these varied across three sessions dependent on observers' responses in previous sessions. In session one, the foveal stimuli varied from -40 to +40° in 10° increments about the constant peripheral hue. The patches were equal in distance from the grey point to equate colour contrast. In session two, the PSE (i.e. angle in colour space at which foveal stimulus perceptually matched the peripheral stimulus) was calculated for each observer, and the foveal patches were varied in 5° increments about this value. In session three, the foveal patch chromaticities varied in 2° increments about the PSE extracted from session two data.

A full screen animated mask consisting of multiple 1.86° circles, within the palette and luminance range of the experiment and randomly changing position and chromaticity at 100Hz, was displayed in between trials to minimise retinal adaptation.
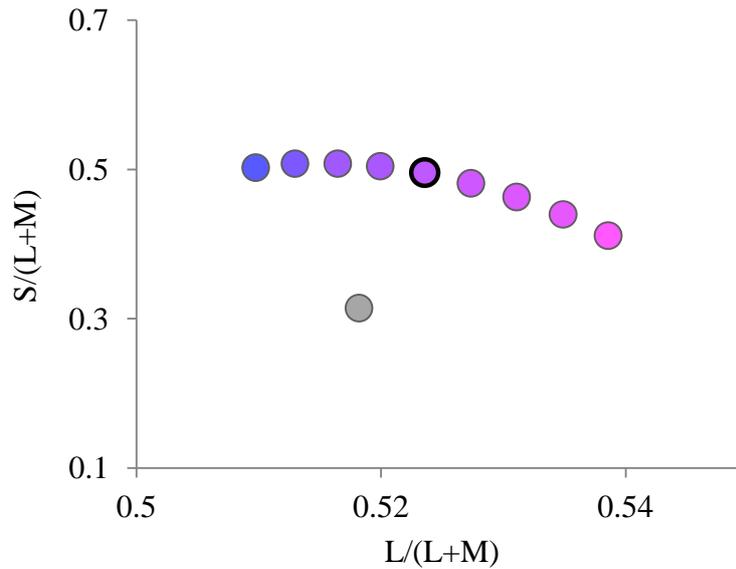
Figure 4.5. MCB chromaticity coordinates for Session 1 of Experiment 4.2. The chromaticity of the peripheral patch remained constant across trials (denoted by the black outline). Nine variable foveal patches vary in 10° increments about this point. Grey point represents the background chromaticity.

2AFC Constant stimulus hue-matching task and procedure

For each trial, the observers' task was to judge whether a foveal patch was 'bluer' or 'pinker' than a peripheral patch, by pressing one of two buttons on the response box. Observers were instructed to continually fixate on the circular frame that had the black fixation dots above and below it. At the start of each trial, the circular frames and fixation dots were presented for 1000ms so that fixation could be acquired. The peripheral stimulus was then presented for 100ms, followed by a blank screen for 1000ms (inter-stimulus interval), and then followed by the foveal stimulus for 100ms.

In the Eyes Stationary condition, the fixation dots remained on the same side of the screen throughout the trial, but the presentation of the peripheral and foveal patches were on opposite sides of the screen. In the Eye Movement condition, the fixation dots switched from the left (or right) to the right (or left) during the inter-stimulus interval so that the observers performed a single saccade between the presentation of the peripheral and foveal stimulus. Thus, the screen location of the foveal and peripheral patches remained constant. After the foveal patch was presented, the observers were able to respond. The mask was then presented for 600ms before the next trial commenced.

Observers completed three sessions of each condition. The first session was always the Eyes Stationary condition, so that observers could adapt to the hue-matching task before the more difficult saccade component was added. After session one was completed, the condition presentation was counterbalanced across observers. Observers received 90 trials, 10 repetitions of each foveal patch chromaticity per session. The position of the peripheral patch (left/right) was counterbalanced. The experiment was run in a dark laboratory. Eye movements were recorded (as described in Chapter 2) and checked offline, and trials were discarded if the observer did not fixate or move their eyes appropriately during the stimulus presentation sequence.

Results and Discussion

Figure 4.6 shows psychometric functions for each observer in the Eyes Stationary condition (a) and the Eye Movement condition (b). Across both conditions most observers display a consistent shift in PSE (red diamonds), so that the foveal stimulus must be physically bluer than the peripheral stimulus in order for them to perceptually match. These results confirm those of Experiment 4.1 and also previous research demonstrating that the physical stimuli in the periphery appear bluer than in the fovea (Boynton et al., 1964; McKeefry et al., 2008; Parry et al., 2006; Weitzman & Kinney, 1969).

No significant difference was found between the degree of the colour shift in the Eyes Stationary and the Eye movements conditions ($t(6) = 0.43$, *n.s.*). Thus we did not find any evidence of a compensatory mechanism that actively adjusts the hue of an object when it changes retinotopic location but remains in the same spatiotopic location. Further, this hypothesis does not appear to explain why we rarely perceive variations in hue across the retina in natural viewing.
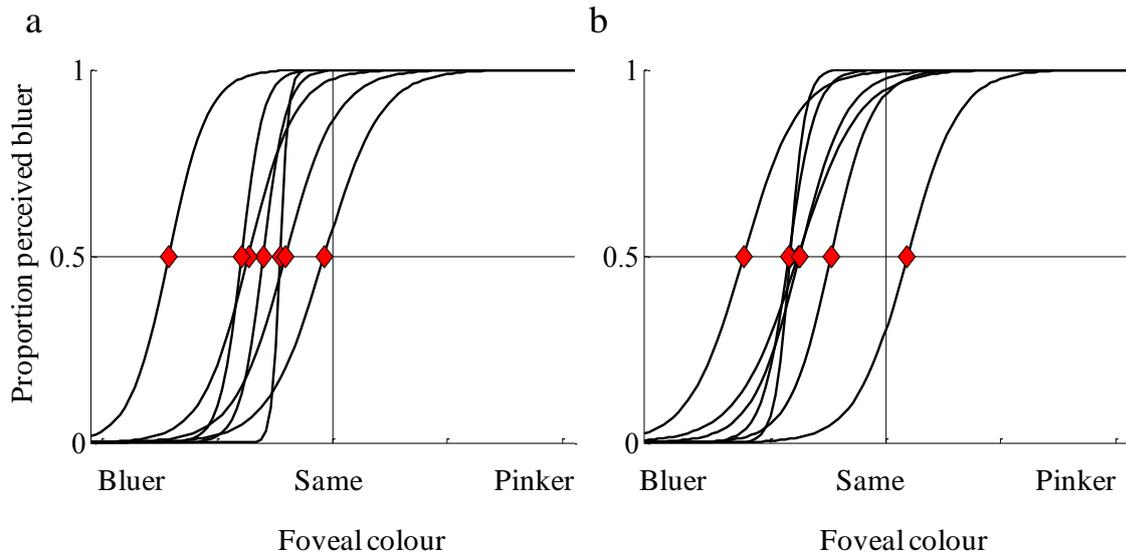
Figure 4.6. Psychometric functions for seven observers in Experiment 4.2 for the Eyes Stationary (a) and Eye Movement (b) conditions. The physical variation in the foveal stimulus are shown along the x-axis, and the proportions of responses that the foveal stimulus was perceived as bluer than the peripheral stimulus is shown along the y-axis. The PSE (physical foveal stimulus that perceptually matches the constant peripheral stimulus) is denoted by the red diamond. All but one observer in each condition shows a shift in PSE towards pinker hues. This means that the foveal stimulus had to be physically bluer than the peripheral stimulus to perceptually match it in both experimental conditions.

Chapter 4 Discussion

Laboratory studies have found perceived hue variations between the fovea and the periphery (e.g. McKeefry et al., 2007; McKeefry et al., 2008; Parry et al., 2006; Parry et al., 2012), yet we do not tend to subjectively experience these variations during every day vision. In this Chapter, we explored the hypothesis that compensatory mechanisms that reduce these colour variations may only be present in natural viewing conditions. We measured fovea-periphery hue differences in two conditions which are more similar to natural viewing. First, by using natural surfaces instead of computer-generated stimuli (Experiment 4.1). Second, by shifting the retinotopic position of the coloured surface with an eye movement instead of moving the surface itself (Experiment 4.2). This condition is more similar to natural viewing because changes in retinotopic location of surfaces are more frequently due to the eyes moving about than to the surfaces moving.

Visual field colour variations for natural spectra

Most previous studies reporting fovea-periphery colour differences have used computer-generated stimuli. However, the profiles of artificial spectra are different to the natural spectra the visual system has evolved, and developed over the lifetime, to process. Natural spectra tend to have a smooth profile of radiance across the spectrum, while spectra generated by a monitor display sharper peaks that correspond to the dominant RGB signals. It is possible that these differences in the spectra would produce differing effects of spectral filtering. However, after measuring fovea-periphery hue differences with two types of natural surfaces, fruit juices (Experiment 4.1a) and Farnsworth-Munsell papers (Experiment 4.1b), we observed shifts in a similar direction to those found with artificial stimuli. Both types of natural surfaces were perceptually shifted towards shorter-wavelengths in the periphery than in the fovea. For the Farnsworth-Munsell papers, the hue shift represents around 0.5-1 JND for most observers.

Since conducting these experiments, this finding has also been reported by (Parry et al., 2012), although these authors used presentations at larger eccentricities than in our experiments (18°). Such large eccentricities are probably outside the range where most colour-driven tasks take place.   Although we have not used modelling in this Chapter to directly compare the magnitude of hue shifts between artificial and natural stimuli, later

research from our lab suggests that the size of the shifts is likely to be similar (see Figure 3C from Bompas et al., 2013).

Examination of the chromaticity coordinates of the natural stimuli suggests that they varied in saturation as well as hue when compared against their respective backgrounds. For both fruit juices and Farnsworth-Munsell papers, the bluest stimuli were closer to the background in MCB space than the pinker stimuli. MLB colour space is based on lower level opponent mechanisms and is not a perceptual space, thus it is possible that the stimuli still appeared equal in saturation. Original verification of the FM test by the developers reported that the caps were perceptually equal in saturation (Farnsworth, 1943; Nickerson & Granville, 1940). Thus, the extent to which the stimuli appeared equally saturated may have depended on other factors such as the degree of adaptation to the local background. Observers were instructed to attend only to hue, which should have minimised the interference of saturation.

Visual field colour variations during eye versus surface movement

During natural viewing, it is usual for the eyes that move while the surfaces in the world remain stationary. The stability of surfaces may allow the visual system to learn about the hue differences of the same objects as eye movements shift them to different positions on the retina. Yet, colour differences across the visual field are often measured in conditions where the eyes remains stationary and either the surface will move or two different surfaces are presented together at different locations. Drawing on ideas of the sensorimotor theory of perception (O'Regan & Noe, 2001), we proposed the existence of an active mechanism, driven to maintain perceptual stability, that compensates for variations in hue of the same surface when an eye movement shifts the surface's position on the retina. Our hypothesis was fuelled by the existence of other mechanisms, such as pre-saccadic remapping, that are activated just before each saccade and influence perception at the post-saccadic location (Melcher, 2007; Wittenberg et al., 2008).

We tested this idea in Experiment 4.2 by comparing the fovea-periphery hue shifts in a condition where the eyes remain stationary and the coloured surface is moved across the retina (Eyes Stationary condition) to a condition where the surface remains in the same spatiotopic location but the eyes perform a saccade to shift the surface to a different retinal position (Eye Movement condition). However, our results were inconsistent with the existence of our hypothesised compensatory mechanism because we found fovea-periphery

hue differences of the same direction and magnitude in both the Eyes Stationary and Eye Movement conditions.

Previous research has shown that contingencies between the direction of eye movements and hue can develop over an experimental session and lead to partial compensation for this introduced bias (Bompas & O'Regan, 2006a, 2006b; Richters & Eskew, 2009). Given that macular pigment density has remained stable since childhood, it is somewhat surprising that similar mechanisms have not compensated for fovea-periphery hue differences. It is possible that compensatory mechanisms are only activated when an abrupt, large bias is introduced. Bompas & O'Regan (2006) used coloured hemi-field goggles to produce a strong chromatic bias and within the experimental session only partial compensation was reported. It is possible that sensorimotor learning is most active during a critical period of synaptic plasticity in infancy and becomes less influential later in life (Bompas et al., 2013). Macular pigment is mostly absent at birth and increases up to the age of around 2 years (Bone et al., 1988), and if learning largely took place before this time, we might expect residual, uncompensated colour biases to persist into adulthood. Thus, although it is possible that sensorimotor learning does help to maintain perceptual stability and reduce biases, this learning may not always be complete and ongoing throughout the lifetime, especially if the biases are small.

Is calibration for retinal colour biases possible?

Calibration for visual field colour biases does not have to be driven by a mechanism that only activates during eye movements. Colour discrimination is not impaired when the targets are spatially separated, which points to the existence of higher level processes that are able to compare colour across space (Danilova & Mollon, 2006). Other research in our lab has explored whether colour biases due to macular pigment are systematic and predictable enough to allow learning and calibration to occur over the lifetime (Bompas et al., 2013). Fovea-periphery chromaticity shifts were measured for a number of natural and artificial surfaces and were found to be highly systematic. Comparison of models that predict no learning about these shifts versus complete learning based on the available information, suggests that the shifts we observe in participants are somewhere in between these two extremes. Thus, although some calibration may have occurred, this learning is less than could be expected given the available information. This finding adds further support to the

possibility of a critical period during infancy in which the majority of the calibration occurs but is also before the full density of macular pigment has developed.

Why do we not perceive these distortions in natural viewing?

The experiments in this chapter tested two possible reasons why we do not perceive fovea-periphery colour variations during natural viewing, but neither provided a definite answer. One possibility is that, just because we observed hue shifts for isolated natural stimuli, this finding would not transfer to complex natural scenes. Scenes in the 'real world' tend to be composed of many different contrast levels, spatial frequencies and chromatic variations, and it is likely that these could mask small differences in hue across the retina. For example, the hue of targets may be influenced local contrast effects (Ekroll & Faul, 2012; William Yund & Armington, 1975). Given the complexity of natural scenes it would be difficult to isolate which factor, or combination of factors, was masking the colour difference.

Another factor that is missed by comparing two isolated coloured patches is the possibility of filling-in and chromatic spreading. As we discussed in the previous chapter, colour is particularly constrained to edges: colour signals will spread across surfaces until they reach an edge and the colour of the edge can determine the colour of the surface within (von der Heydt et al., 2003). In natural viewing, if a surface large enough to bridge across the fovea and periphery, local filling in, spreading, or averaging effects could promote retinal homogeneity. Indeed, research has suggested that for large colour fields, perceived hue is an average of the centre and periphery (Vienot, 1983). Future research could explore this suggestion by testing conditions in which a continuous surface is provided between the foveal and peripheral comparison targets.

It is also possible that we simply do not notice these colour biases because the difference in hue when an object changes retinal position from fovea to periphery is not salient enough to grab our attention. There is a long literature on the how attention influences our ability to notice changes in the environment, and these effects are illustrated in the phenomena of change blindness and inattentional blindness (Simons, 2000; Simons & Chabris, 1999; Simons & Rensink, 2005). The experiments in this Chapter used purple hues that should evoke the largest, most salient, fovea-periphery differences. Despite this, in Experiment 4.1b, we found hue shifts that were only around one JND in size and it could be argued that this would not be salient enough to seize attention. Shifts for other hues may be even smaller and

less noticeable, and these hues are also probably more frequent in natural scenes than the purple range we used in our Experiments.

Related to this last suggestion, previous work has found that achromatic surfaces may be perceptually invariant across the retina (Beer et al., 2005; Parry et al., 2006; Webster et al., 2010). This is probably because short and long term adaptation mechanisms normalise the ratio of retinal activity to the average stimulation (Webster & Leonard, 2008). Similar processes contribute to colour constancy under different illuminations (Smithson & Zaidi, 2004) and also compensate for internal biases such as thickening of the yellow crystalline lens later in life (Schefrin & Werner, 1990; Werner & Schefrin, 1993; Wuerger, 2013). As noted earlier, however, this adaptation would not be able to remove colour biases that are specific to certain regions of the retina for all hues, because different hues are effected to different extents by macular pigment filtering.

In the General Introduction we discussed other factors may also contribute to colour differences alongside macular pigment, which is probably the most important factor. These include increased rod contributions, decreased density of L and M cones, and more random sampling of cones by ganglion cells in the periphery. The exact cause of the colour distortions is not important for findings of this Chapter, however, as we were only concerned with whether they still exist under natural viewing conditions. The different factors could influence the time-scale over which learning could take place and the extent to which the distortions can be calibrated away within a critical period. However, both macular pigment and cellular populations/connections are likely to be connected to the development of the retina and thus have similar time frames.

Results within a Bayesian framework

Chapters 2 and 3 were concerned with how ambiguous afterimage signals are interpreted by the visual system by using information from prior experience. For example, real objects often have sharp luminance edges and tend not to move with the eyes. These prior expectations are then used to interpret an ambiguous afterimage signal. Although we did not mathematically model our theory, it is rooted in Bayesian theory. If we apply these ideas to retinal colour differences, it could be argued that peripheral signals tend to be more ambiguous than foveal signals and thus would be more influenced by prior expectations. However, in terms of colour differences across the retina, the learning we have previously discussed and the prior

expectation would both predict the same thing: there should not be a colour difference between the fovea and the periphery. Thus, the logic follows that learning is incomplete, or to use Bayesian vocabulary, that the prior does not drive the perception completely. We use the phrases 'continuous learning' and 'calibration' in this Chapter because colour differences are a stable, ever present distortion unlike afterimages that are intermittent, discrete perceptual events.

In terms of specific influences on colour, a prior could shift perception towards an average in the environment. In most environments this shift would be towards achromatic colours. This is consistent with previous research that surfaces in the periphery appear desaturated in comparison to the fovea (Gordon & Abramov, 1977; McKeefry et al., 2007). Although, it should be noted that there low-level physiological explanations for these saturations effects have been suggested (McKeefry et al., 2007). We would not expect a prior capable of shifting perception towards a particular hue as these would change with the environment (e.g. forest, desert, urban) and within the environment (e.g. ground, sky).

Summary

In this Chapter we were interested in why colour variations across the retina are observed in laboratory conditions but not in everyday life. We tested two possible natural viewing conditions that could lead to compensation for these colour variations. Experiment 1 found that hue shifts between the fovea and periphery are still observed for natural spectra (fruit juices and Farnsworth-Munsell papers). In Experiment 2, we found that hue shifts are still found when an eye movements shifts the positions from the surface between the fovea and periphery rather than when the surface itself moves. These results suggest that if a compensatory mechanism exists during natural viewing it was not identified by the experiments in this Chapter. In the Discussion, we identified some of these other factors, including the complexity of natural scenes and attention.

Chapter 5: General Discussion

Overview

The central aim of this thesis was to explore what determines our conscious perception of two phenomena, neither of which represent meaningful properties of the world but originate only on the retina. Our perception of these phenomena was of interest to us because it raised the question of why we perceive something that is not a physical property of the world. The purpose of studying the conditions under which these phenomena are, and are not, perceived was to inform us about the strategies used by the brain to guide perception.

In Chapters 2 and 3 we explored different cues that influence the perception of afterimages. Our hypothesis was that afterimage signals are inherently ambiguous to the visual system and therefore would be highly influenced by any cues that either increased or decreased the likelihood that they represent a real object. The experiments in Chapter 2 revealed that afterimages are enhanced by contextual edges more than real stimuli of similar appearance, which would support the idea that afterimage signals are more ambiguous than signals originating from real objects.

Chapter 3 built on this idea and explored the influence of different types of eye and lid movements on afterimage visibility. We hypothesised that saccadic eye movements would shift the afterimages around the world in a way that was unlike any real object and thus would lead to afterimage suppression. Our results supported this prediction as saccadic eye movements reduced afterimage duration more than conditions where the afterimage did not move unnaturally, for example, during fixation, pursuit and blinking. In Chapter 3 we also found that contextual edges and saccadic eyes movements are combined additively in their influence on afterimage duration, although the edges may dominate the perceptual interpretation of the afterimages in the first instance.

Our attention shifted to another phenomenon in Chapter 4 - colour variations across the visual field produced by spectral filtering differences between the fovea and the periphery. We were interested in why these colour variations are evident in laboratory studies and yet are seemingly absent from everyday viewing. We hypothesised that compensatory mechanisms

may exist only in conditions that are more similar to natural viewing. To test this idea, we measured colour variations with natural spectra and during eyes movements, but found classic fovea-periphery hue shifts in both conditions. Our conclusion was that perhaps our 'natural' conditions were still not as 'natural' as real world scenes, and that other factors, such as attention, may highly influence our perception of these colour differences.

Ambiguity/likelihood theory of afterimage perception

Afterimages have held the interest of scientists and philosophers over many centuries. They have been used as tools to probe a number of features of the visual system, and have remained of interest simply as illusory phenomena and good fodder for visual illusions. Most afterimages are produced by adaptation of specific classes of retina cells, but our perception of them appears to be highly influenced by higher level processes. Of course, retinal signals that originate from viewing real world objects are also subject to additional processing, but we speculated that afterimage signals may be particularly open to perceptual interpretation. This speculation was inspired by the perceptual instability of afterimages – they can fade in and out of conscious awareness. This, coupled with compelling demonstrations of how afterimages can be rendered visible by consistent contexts and invisible by inconsistent contexts, lead us to hypothesise that afterimages may not be just another example of a faint, blurry percept.

This idea is novel; even the most recent studies of afterimages have explicitly predicted that to cells in the LGN and visual cortex, afterimage signals are indistinguishable from any other signals sent from the retina (Zaidi et al., 2012). In contrast to this, we hypothesised that afterimage signals may be fundamentally ambiguous because the nature of their responses is different to signals arising from real objects. Due to the added ambiguity of afterimage signals, we predicted that they would be particularly susceptible to cues that either increase or decrease the likelihood that they represent a real object. In Chapters 2 and 3 we studied two possible examples of these cues: contextual luminance edges and eye and lid movements.

Contextual luminance edges

Using a matching and a nulling paradigm, the experiments in Chapter 2 found that both luminance and colour afterimages are enhanced by sharp luminance edges more than physical

stimuli of similar appearance. Control experiments revealed that this effect could not be explained by differences in the degree of edge blur between the afterimages and the real stimuli, nor differences in the onset of the contour relative to the onset of afterimage and real stimulus signals. It is known that luminance edges can constrain and enhance chromatic signals perceptually (Chaparro et al., 1994; Cole et al., 1990; Eskew Jr et al., 1994; Gur & Akri, 1992; Hilz & Cavonius, 1970; Hilz et al., 1974; Montag, 1997; Mullen & Losada, 1994) and there is evidence of joint colour-edge cells in the visual cortex that could underlie these effects (Horwitz et al., 2005). However, the finding that afterimages are enhanced by luminance context more than signals arising from real objects lends support to our hypothesis that afterimage signals are more ambiguous and so more influenced by cues that help to guide the perceptual interpretation in one direction or another.

Eye movements

The Experiments in Chapter 3 explored the historical notion that saccadic eye movements suppress or change afterimage perception. We began by critically evaluating different theories for why saccadic eye movements might have this effect, including those that have suggested that saccadic eye movements produce physiological changes on the retina and changes to the retinal image that disrupts adaptation, and that afterimages may be suppressed by classic saccadic suppression mechanisms.

We designed a series of experiments to test one particular theory, first proposed by Exner (1890), that afterimage perception is suppressed by saccadic eye movements because they cause the afterimage to move about in a way that is unlike a real object. Based on this theory, our hypothesis was that afterimage perception would be reduced by saccadic eye movements but not by other eye and lid movements, such as pursuit and blinking, which do not produce unnatural afterimage movements. Consistent with this, we observed that both afterimage duration and the likelihood of perceiving an afterimage at all was reduced during saccades relative to fixation, pursuit or blinking.

Context and eye movement interactions

In Chapter 3 we were also interested in how luminance edges and saccadic eye movements would interact in their influence on afterimage perception. Specifically, our aim was to determine if one cue would dominate the perceptual interpretation, or whether the effect of both cues would be additive. After efforts to match the degree of contour alignment during

fixation and saccadic eye movements, we found that the effect of the luminance edge and saccadic eye movements on afterimage duration was probably additive. Thus, afterimage duration was lengthened by the addition of a surrounding luminance contour, but at the same time, could be shortened if saccadic eye movements were performed. In comparison, we observed a significant interaction between the contour and saccades in the measure of whether an afterimage was seen at this. Thus, the contour decreased the probability an afterimage was seen at all relatively more than the saccades increased this measure. This suggests that luminance edges are perhaps more dominant in influencing the first decision of whether to perceive the afterimage or not than the saccades.   Overall, the effect of the contour on afterimage intensity is stronger than the effect of the saccades. It is possible that if the afterimages were longer and thus allowing time for a greater number of saccades, the effect may increase. Research involving stronger afterimages, similar to those used in previous studies, is needed to test this suggestion.

What is the source of afterimage ambiguity?

Although we have not explored directly ways that the pattern of activation that produces an afterimage may be different from that arising from a real stimulus, it is possible to consider some likely candidates. We have already discussed that eye movements, particularly saccades, could decrease the likelihood that an afterimage signal represents a real object. For this reason, the experiments in Chapter 2 were conducted with the eyes fixed to minimise the perceptual difference between afterimages and real stimuli created by eye movements.

It is possible that even though we restricted larger eye movements in Chapter 2, small fixational jitter may have been sufficient to reveal that the afterimage percept was illusory. This knowledge could arise from compensatory mechanisms that stabilise the retinal image based on whole-world motion during jitter (MraKami & Cavanagh, 1998). These compensatory mechanisms would lead to a discrepancy between the afterimage movements relative to the background. The contour could have enhanced the perception of the afterimage because it provided a visual transient that is similar to the edge of a real object, and this transient would dominate the weaker signal that the afterimage itself moves with the eye-jitter. If jitter were to become too large, however, it is likely that it would dissociate the moving afterimage from the stationary contour (by providing an extra background reference), and thus the enhancement effect would be lost. This is why we attempted to minimise the

discrepancy in contour misalignment between the fixation and saccade conditions in Chapter 3, when exploring contour-eye movement interactions.

Apart from eye movements, we also controlled for many other possible perceptual differences between the afterimages and the physical stimuli, e.g. they were matched for hue, luminance, edge blur and saturation. Controlling for these factors means it is possible to consider the existence of other critical factors differentiating the representation of afterimages from that of real stimuli of similar appearance.

First, the temporal profile of an afterimage response is likely to be different from that representing a real stimulus. For example, the change from adaptor to afterimage (i.e. the off response) is unlikely to be exactly the same as the onset of a new stimulus. This difference could potentially underlie the experience of a small delay before the afterimage percept appears after the adapting stimulus is turned off (Creed & Graniy, 1928). Similarly, the exponential recovery from adaptation (McLelland, Baker, Ahmed, & Bair, 2010) is unlikely to exactly mimic the activity profile displayed when viewing a real stimulus. Second, if adaptation is present at multiple colour-sensitive sites throughout the visual system, cells in these sites may have different cellular architectures, different susceptibilities to adaptation, and their relative recovery from adaptation could occur at different speeds (Fairchild & Reniff, 1995; Jameson, Hurvich, & Varner, 1979; Loomis, 1972; McLelland et al., 2009; Rinner & Gegenfurtner, 2000; Yeh, Lee, & Kremers, 1996). This means that the relative firing rates after adaptation will differ between areas in a way that is inconsistent with how real stimulus signals elicit activity patterns through the visual system.

Loci of adaptation

The sites of adaptation that may contribute to generating colour afterimages are worth discussing here as this has been the subject of much debate. Past research has variously championed the existence of afterimage-generating adaptation in the photoreceptors (Brindley, 1962; Craik, 1940), retinal ganglion cells (Virsu & Laurinen, 1977; Zaidi et al., 2012) and the cortex (Shevell, St Clair, & Hong, 2008; Shimojo, Kamitani, & Nishida, 2001). However, most previous research suggests that the adaptation is likely to be constrained to the retina.

We can identify three possible sites of adaptation - although our results are consistent with any or all of these and do not exclusively point to a cortical locus. Firstly, because we found that edges enhance afterimages more than they do physical stimuli, we could assume some adaptation at the level(s) at which edges enhance chromatic signals. As discussed earlier, this is likely to be cortical. Secondly, it is possible that although the edge first facilitates chromatic signals in the cortex, feedback signals are subsequently relayed back to the LGN to amplify and tune its response (Ferster & Miller, 2000). This means that cortical influences that are responsive to the luminance edge, such as fine orientation tuning and attention, could evoke relative changes in LGN activity. Thus, adaptation responses in the LGN could be enhanced by edge-driven amplification by the cortex. Finally, higher level visual areas may be sensitive to temporal differences between retinal ganglion cell rebound signals resulting from adaptation and those arising from real stimuli. Thus, these ganglion signals may be more susceptible to edge enhancement because they deemed more ambiguous or unusual by higher levels. As noted above, our results do not distinguish between these suggested adaptation sites, only that at some point the visual system is able to dissociate signals arising from adaptation from those representing real objects.

Types of afterimages

The experiments reported here examined the duration of faint, negative afterimages viewed against illuminated homogenous backgrounds. Our findings from Chapter 3 with this type of afterimage are relatively novel, as much of the previous work investigating the effect of eye movements on afterimage perception have used intense positive afterimages viewed in the dark (Fiorentini & Mazzantini, 1965; A. H. Friedman & Marchese, 1978; Kennard et al., 1970). As discussed in the General Introduction, an intense afterimage is likely to be generated from different mechanisms on the retina than a less intense afterimage. Intense afterimages probably arise from intense adapting stimuli that bleach cone photoreceptor cells, while less intense afterimages from less intense adapting stimuli are more likely to be due to retinal ganglion cell rebound signals (Zaidi et al., 2012). The polarity of afterimages depends on whether they are viewed against dark backgrounds (positive) or light backgrounds (negative). The different states of the retina that generate these afterimage perceptions could lead to subtle differences in how eye movements interact with the afterimages. Indeed, Kennard et al. (1970) reported that negative afterimages (they referred to them as 'transductive' afterimages) were not subject to disappearance after saccades, while positive

afterimages were (which they named 'emissive' afterimages). It is possible that the effect of saccadic eye movements on afterimage duration is stronger for positive afterimages than for negative afterimages, which could explain Kennard's findings. Further research is needed however, to clarify whether, and why, this is the case. However, our findings add further confirmation to the literature that saccades lead to a reduction in perception across a range of different afterimages types.

Colour variations across the retina

Chapter 4 focused on a different 'illusory' percept that is produced on the retina - colour variations across the visual field. Macular pigment is a spectral filter present only in the fovea and causes perceived colour biases between the fovea and the periphery where surfaces in the periphery are shifted towards shorter wavelength hues. These colour differences are similar to afterimages in that they are easy to demonstrate in laboratory conditions yet are mostly absent from everyday vision. Unlike afterimages, the root cause of centre-periphery colour differences, macular pigment, remains fairly stable in the adult retina. Thus, it is somewhat surprising that these differences have not been calibrated away and that we are still able to observe them in the laboratory. This led us to hypothesise that compensatory mechanisms may only be activated in, or calibrated for, natural viewing conditions. In Chapters 2 and 3 we reported that cues that are present during natural viewing, context and eye-movements, can influence our perception of afterimages. In Chapter 4 we examined the influence of two natural viewing cues on our perception of fovea-periphery colour differences.

Natural viewing conditions

We first measured fovea-periphery hue shifts using natural surfaces instead of computer-generated stimuli. It is possible that the visual system has adapted through evolution, or learnt over each lifetime, to compensate for differences in natural spectra but not differences in spectra it is less exposed to. Contrary to this, we observed fovea-periphery hue shifts in the same direction as found with computer-generated stimuli using two types of natural surfaces, fruit juices and Farnsworth-Munsell papers.

Natural spectra are only one component of what makes natural scenes different from laboratory presentations. Natural scenes are highly complex and tend to be packed with variations in local contrast, hue and spatial frequency. Any of these alone or in combination could drive the reduced perception of colour variations during natural viewing. However, an experiment that was able to isolate the exact mechanism, or combinations of mechanisms, would be difficult to design due to the complexity of natural scenes.

The second difference between laboratory studies and natural viewing we tested was the inclusion of eye movements to shift the position of the surface on the retina. During everyday vision the eyes roam around while objects in the world remain mostly stable. This viewing procedure is the exact opposite to how most laboratory experiments are run. One way the visual system could learn to compensate for fovea-periphery hue differences is by sampling the same objects at different positions on the retina. Our hypothesis was that compensatory mechanisms may only be activated when the eyes move and it is clear to the visual system that the same surface is being viewed before and after the eye movement. We compared fovea-periphery hue shifts in conditions where the eyes remained stationary and the coloured surface moved from the periphery to the fovea, to when the surface remained in the same spatiotopic position, but the eyes moved to switch its position on the retina. Contrary to our predictions, however, we did not observe a difference in the direction or magnitude of hue shifts between these two conditions.

Thus the two more 'natural' conditions we tested did not provide an answer to why fovea-periphery colour differences are not perceived during every day vision. As discussed in Chapter 4, there may be many other possible answers to this question. We may not notice these differences because attention is a limited resource that is biased towards the most salient features and colour differences are small in magnitude and only affect certain hues. As previously mentioned, there are also many features of complex natural scenes that could influence chromatic adaptation and perception beyond the ones we tested. Despite the limited conclusions that can be drawn from the experiments in Chapter 4, we have been able to confirm the existence of fovea-periphery hue shifts in these more natural settings. The experiments also provoke thought about the difficulty of marrying laboratory findings to perception in the natural world.

To see or not to see: That is perception

Most vision research is concerned with how we form a representation of the world from the continual stream of the light entering the eyes. The field of psychophysics is based on the principle of comparing the physical to our perception of the physical. The experiments in this thesis have examined perception in the absence of a physical stimulus. The advantage of using these illusory perceptions is that they immediately provoke questions about why we perceive them; at some point the visual system has made a perceptual decision one way or the other. Of course, this statement is true for most sensory signals passing through the visual system; the difference with the illusory phenomena explored here is that there are ways to distinguish them from signals arising from real objects. Afterimages move with the eyes unlike any real object, colour differences are highly systematic and we are able to compare colours across space. Thus it could be argued that if vision was entirely optimal we would never perceive an afterimage or a colour difference across the retina, or indeed, anything that was not real.

This view is, however, over-simplistic because it fails to acknowledge that the mechanisms at the source of these illusory phenomena may serve a useful purpose that outweighs the cost of perceiving something that is not real. This idea is by no means novel; our perception of many visual illusions is described as generally useful mechanisms providing a rare 'wrong' answer in a highly artificial and ambiguous situation (e.g. Weiss et al., 2002). Our perception of afterimages is of particular ecological interest because in natural viewing we do adapt for long enough to develop afterimages and afterimages are sometimes perceived. Thus, in a sense, the 'artificial' component is comparatively small and there is little perceptual trickery involved in their creation.

Studying the different influences on afterimage perception provides a glimpse into how the visual system interprets ambiguous information. It demonstrates the power of higher level cues in biasing perceptual awareness. The brain might be aware that there is something 'unnatural' about an afterimage signal; it moves with the eyes, it decays exponentially, it may not be consistent across different levels of visual system. Yet place a strong, non-ambiguous contour around it and suddenly the perceptual likelihood that it should be perceived increases. Make saccadic eye movements and suddenly this perceptual likelihood decreases. In natural viewing there may be countless other influences on our perception of afterimages that we have not yet identified. We suggest that our experiments with afterimages add support to the suggestion that the brain is a perceptual detective, collecting and balancing evidence for and against different interpretations.

It more surprising that colour variations across the retina have not been vanquished from awareness because they are a more constant, stable bias in perception than afterimages. They raise interesting questions about the effects of critical periods during infancy and childhood where greater neuroplasticity allows for fuller calibration. They also raise the question of whether biases are only compensated or calibrated away if they are salient enough to be noticed and when the cost of miscalibration is high. There are many other situations where perception remains uncompensated. The blind spot is perceptually 'filled-in' in the visual cortex, but no mechanism exists that is able to retrieve the lost information (Komatsu, Kinoshita, & Murakami, 2002; Magnussen, Spillmann, Stürzel, & Werner, 2004). This is different from compensation for macular pigment, where in a sense, information is 'biased' but not lost completely, and more compensation than is observed would be possible given the predictability of the bias (Bompas et al., 2013). There are examples of 'illusions' in 3-D space perception that may remain uncompensated (Cuijpers, Kappers, & Koenderink, 2003; Wolfe, Maloney, & Tam, 2005), although these could reflect optimal combinations of available evidence (Hogervorst & Eagle, 1998). Clearly more research is needed to clarify the extent to which miscalibrations underlie other processes that are useful, and even optimal, versus the extent to which they expose the limits of the visual system to continually learn from experience in the world.

Future directions

Stabilised images

In Chapter 3 we discussed that saccadic eye movements cause both afterimages and other stabilised images to disappear. A question remains about the extent to which an afterimage is just another example of a stabilised image. We suggested that the retinal stability of afterimages may be one contributing factor to their ambiguity, but we also suggested other factors such as temporal features of recovery from adaptation and the inconsistency of signals across visual areas. One interesting question is whether stabilised images are enhanced by luminance edges to the same extent as afterimages are, or whether they are affected to a similar extent as signals arising from real objects. Investigating this question may allow us to pinpoint exactly what causes afterimages to be enhanced by luminance edges more than real stimuli of similar appearance. The ideal design of such an experiment would be to stabilise

the blurry physical stimuli we used in Chapter 2 by using a gaze contingent presentation. However, even the best eye trackers (and contact lenses) are not capable of perfect stabilisation so it is possible that we may never be able to answer this question.

Clinical populations

There is the possibility of applying some of the ideas in this thesis to a number of clinical populations. Posterior cortical atrophy (PCA) is a form of Alzheimer's disease that develops first in the occipital lobe. Case studies have reported that the condition may be associated with heightened perception of afterimages (Chan, Crutch, & Warrington, 2001). Individuals with PCA may experience afterimages of much longer durations than typically reported and their afterimages may also begin to colour non-natural surfaces (i.e. when context is inconsistent with the afterimage). Thus some consequence of the disease progression may prevent inconsistent contextual cues from suppressing the perception of afterimages. Chan el al., (2001) suggest that atrophy of certain classes of neurons lead to an imbalance between inhibitory interneurons and neurons responding to the adapting stimulus. This imbalance leads to the development of afterimage signals that are particularly intense. It would be interesting to explore the perception of afterimages in individuals with PCA further and establish the conditions under which these afterimages are perceived, the extent to which they are comparable to retinal afterimages, and whether compensatory mechanisms begin to develop that suppress the perception of them as the disease progresses.

Another possible area of clinical translation is Autism Spectrum Conditions (ASC), which are typically characterised by abnormal social communication and an increased occurrence of repetitive behaviours. Researchers have explored differences in how contextual information is combined in ASC (Bolte, Holtmann, Poustka, Scheurich, & Schmidt, 2007; Dakin & Frith, 2005; Kourkoulou, Kuhn, Findlay, & Leekam), and more recently, differences in how prior knowledge is used to guide behaviour and perception in ASC (Pellicano & Burr, 2012). One hypothesis is that individuals with ASC avoid situations of ambiguity because they have developed less intense prior expectations about the world that would allow them to cope with these situations. It would be interesting to explore this suggestion further through comparing the influence of disambiguating cues in ambiguous situations in typically developed participants and participants with ASC. It would be important to establish whether individuals with ASC display a less intense influence of prior knowledge across all areas of visual processing or whether it is confined to certain pathways. For example, the contextual

influences on afterimages are likely to occur at a fairly low level of visual processing (early visual cortex), which may not be comparable to effects observed in higher visual areas, such as those mediating face and motion processing.

Calibration and prior knowledge in development

Although the building blocks for many visual functions are innate, we have become increasing aware that much of the system that allows us to interpret sensory information must be developed in infancy. The combination of haptic and visual information, for example, may not be optimal in childhood as it is later in adulthood (Gori, Del Viva, Sandini, & Burr, 2008). This raises exciting questions about how the system develops, and leaves one pondering about the nature of infant perception. It is possible that infants may not perceive many of the illusions that adults do simply because their young brains have not developed the strategies and knowledge that these illusions target. Perhaps infants perceive afterimages much more intensely than adults do because cues such as saccadic eye movements are less meaningful in disambiguating what is real and what is not. The critical period for compensation for colour differences across the retina also raises the important question of the extent to which adaptation to our environments is confined to infancy versus the extent to which calibration is ongoing. These questions may be difficult to explore without conducting experiments with younger participants, however these come with the difficulty of attaining reliable perceptual judgements at an age before verbal communication.

Conclusion

The experiments in this thesis have explored how different cues can influence our perception of two illusory phenomena, afterimages and colour variations across the retina that are generated on the retina and bare no relation to a real world objects. In Chapter 2 and 3 we explored the influence of context and eye movements on our perception of afterimages. We hypothesised that the signal representing afterimages are inherently ambiguous and this leads to perceptual uncertainty over whether to perceive the afterimages. We reported that contextual luminance edges increase the likelihood of perceiving an afterimage. While saccadic eye movements, which cause an afterimage to move across the retina in a way that is unlike real objects, decrease the likelihood of perceiving an afterimage. Chapter 4 examined whether colour variations across the retina, mainly produced by macular pigment, are still

perceived under two conditions that are more similar to natural viewing. Results showed that colour differences are still observed with natural spectra and during eye movements, which suggests that these two cues are not the reason that we do not perceive these distortions during everyday viewing. Taken together, the experiments in this thesis add to the growing understanding of how different cues, prior knowledge about the world, and ongoing calibration influences our perception of ambiguous sensory information.

Appendix: Supplementary demos and pilot experiments

A1: Pilots to establish parameters of the contour effect.

Before conducting the experiments reported in Chapter 2, we designed two pilot studies to determine the optimal conditions for observing an enhancement of afterimages by luminance edges. Although previous illusions and experiments demonstrate the compelling effects of luminance edges and context on afterimages, there is little research that directly manipulates lower level features of the effect. Our aim was to establish some of these so that experimental designs in Chapter 2 and 3 could be optimised.

Experiment A1a: Foveal versus peripheral presentation

It was important to explore any differences between foveal and peripheral presentation of the afterimages and luminance edges because both were used in Chapter 2. It has previously been reported that both negative and positive afterimages are more intense and last for longer in the periphery than the fovea (Brindley, 1962; Creed & Graniy, 1928; Matteson, 1965). Although this finding is not consistent across all studies (Trezona, 1960; Washburn, 1900). Thus, in the first pilot we aimed to measure differences in afterimage saturation and the size of the contour effect between foveal and peripheral presentation, using the same adapting stimuli that were used in Chapters 2-3. Four observers completed the same nulling procedure as in Experiment 2.2, but with an added peripheral session in which the adapting stimulus and contour were presented 3° to the left or right of central fixation. The nulling patches had sharp rather than blurred edges; however, this would be more likely to underestimate than overestimate the size of the contour effect on afterimages.

There were a total of 28 trials types within each session (foveal vs peripheral presentation) in a 2 (adaption hue) x 2 (contour presence) x 7 (nulling patch hue/saturation) within-subjects design. Observers received ten repetitions of each trial type, totalling 280 trials. In the peripheral session, presentation was also randomised between left and right.

Individual results from four observers are shown in Figure A.1. A fairly consistent contour enhancement effect is found for both the foveal and peripheral presentation across all observers, in that a more saturated physical stimulus was required to the null the afterimages when a contour was presented. Peripheral afterimages without a contour were more saturated than foveal afterimages for three observers. For two out of the four observers, no foveal afterimage was seen at all when a contour was not presented. Contour enhancement of the afterimages appears to be larger in the fovea for two observers, and relatively equal between the fovea and periphery for the remaining two observers. Taken together, these results suggest that a contour enhancement effect of afterimages can be observed both in the fovea and the periphery. Thus, we were confident in using both foveal and peripheral presentations in the experiments reported in Chapter 2. It is likely that foveal afterimages are weaker than peripheral afterimages, consistent with previous research (Brindley, 1962; Creed & Graniy, 1928; Matteson, 1965). Finally, there is little consistent evidence in this sample that the degree of contour enhancement changes between the fovea and the periphery.
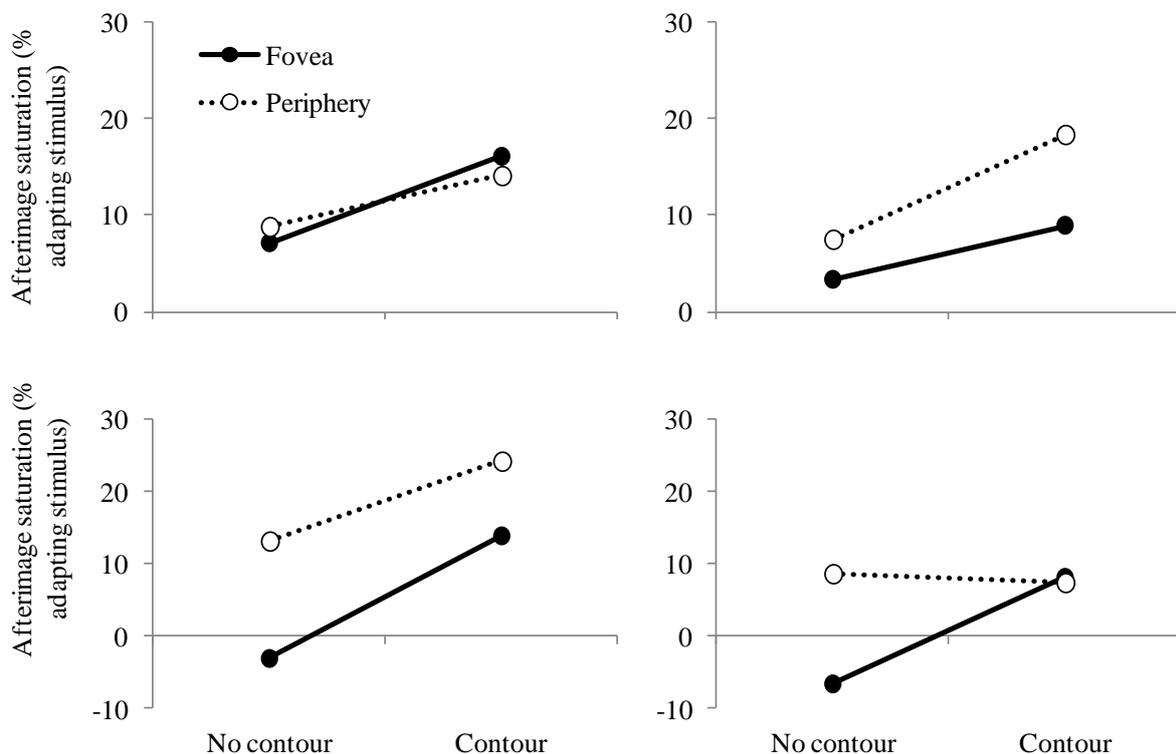
Figure A.1. Individual results from four observers in Experiment A1a. Afterimage saturation (% of adapting stimulus saturation required to null the afterimage) for four observers is plotted for the no contour and contour conditions (x-axis) and also in the fovea (black line) and periphery (dotted line) presentation sessions.

Experiment A1b: Contrast of the luminance contour

The aim of the second pilot was to establish if the contrast of the contour influenced the degree of afterimage enhancement. The only previous research exploring this question is presented in a poster format (van Boxtel & Koch, 2010), in which the authors reported that intermediate contour contrasts produce the largest increases in afterimage duration (see Figure A.2 for a graph of van Boxtel & Koch's results). This is somewhat surprising because it might be expected that the more intense the edge signal the greater the enhancement of the afterimage. However, both filling-in of real colours and van Lier et al's afterimage illusion work for illusionary contours produced by Kanizsa shapes (Feitosa-Santana, D'Antona, & Shevell), suggesting that the physical contrast of the edge is not the only critical factor. It is methodologically more efficient in our experiments to use a contour of lower contrast as this reduces the chances of carryover effects from the adapting to the contour itself. Thus, we were motivated to find the lowest contrast of the contour that would produce a robust afterimage enhancement effect.

Four observers participated in Experiment A1b and the design was similar to the foveal condition in Experiment A1a (i.e. nulling paradigm). However, in addition to a no contour condition there were five levels of contour contrast. Four of the contrast levels were consecutive logs steps from the background luminance based on a Weber fraction of 0.1 (background $28.8cd/m^2$; log steps: 25.92 22.753, 19.267, $15.434cd/m^2$) and the fifth variation was the 7th log step away (or the one closest to black, $1.476cd/m^2$). There were a total of 84 trials types in a 2 (adaption hue) x 6 (contour presence) x 7 (nulling patch hue/saturation) within-subjects design. Observers received ten repetitions of each trial type, totalling 840 trials over two sessions. Trial-type presentation was randomised.
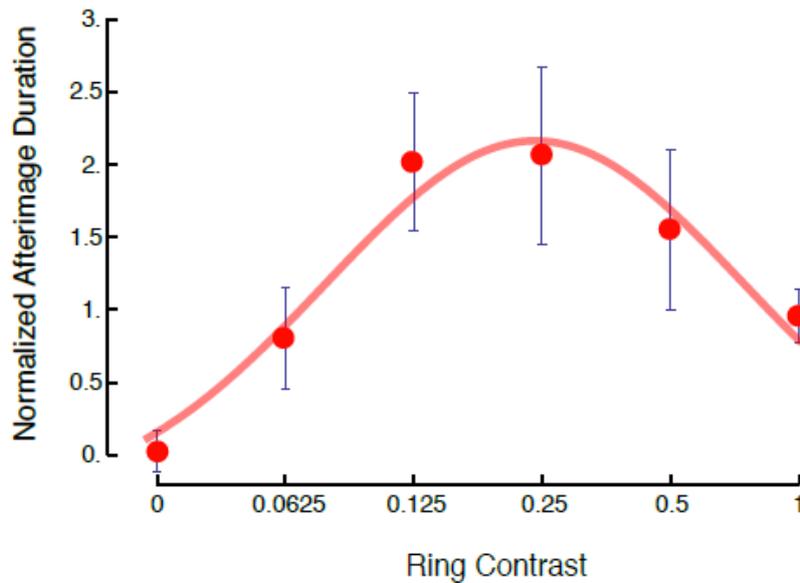
Figure A.2. Effect of contour contrast on afterimage duration as reported by van Boxtel & Koch (2010). Afterimage duration increases with the contrast of the 'ring' (contour) up to a certain point, and then declines with increasing 'ring' contrast.

As seen in Figure A.3, the contour starts to increase afterimage duration relative to the no contour baseline after the second log step in contrast away from the background luminance. However, after this increase the effect plateaus and neither increases nor decreases with increasing contour contrast. Our results are consistent with those of van Boxtel & Koch (2010) insofar as we found that contours of intermediate contrast can enhance afterimages, although we did not observe the same decrease in enhancement with increasing contour contrast. It is unclear what could have driven this inconsistency, but perhaps it is due to methodological differences, e.g. van Boxtel & Koch used a duration measure whereas we used a nulling paradigm. However, because van Boxtel and Koch have only presented their findings in a poster at present, there is insufficient information about their methodologies to speculate further.

Van Boxtel and Koch (2010) suggested that the contour effect on afterimages cannot be explained solely by attention because higher contrast contour would be expected to grab attention more than intermediate contrast contours. Because we did not find an advantage of higher contrast contours, our results would also support this idea. Our findings that a contour of intermediate contrast produces a robust enchantment of afterimage saturation, combined with the fact that contours of lower contrast result in less adaptation to the contour itself, lead to us using a contour of intermediate contrast Chapter 2 and 3.
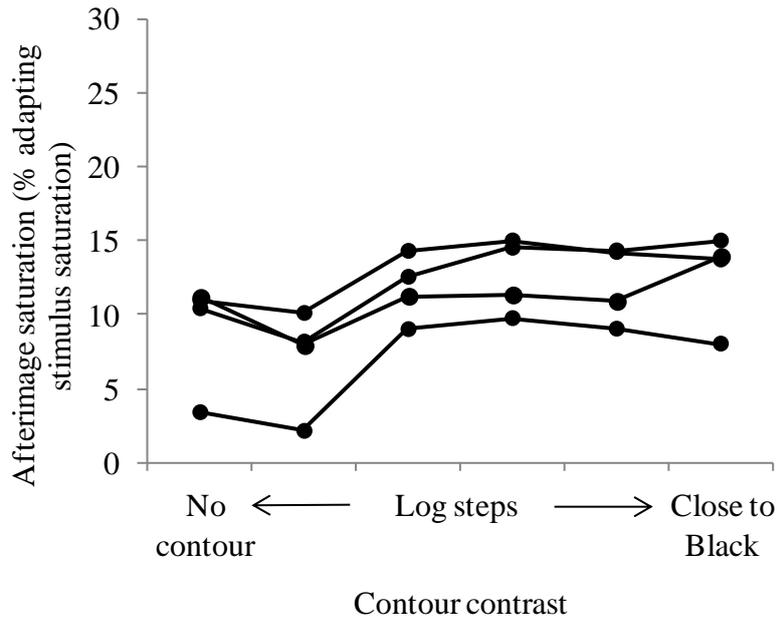
Figure A.3. Results of Experiment A1b which show the effect of contour contrast on the degree of afterimage enhancement. Afterimage saturation (% adapting stimulus saturation required to null the afterimage) is plotted against six levels of contour contrast. All four observers (indicated by separate lines) show a similar pattern: afterimages saturation does not increase from No Contour baseline at the first contrast step. After this, it immediately increases and also plateaus across increasing contrast steps (including one close to black).

A2: Afterimage demonstrations

Demonstrations showing the effect of luminance edges on afterimages and real stimuli are described below and can be found here: https://sites.google.com/site/georgiepowell/

Demo 1: Basic contour effect

Fixate the black dot, you will then be adapted to a pink circle followed first by a contour and then by no contour. The afterimage should appear stronger when framed by a contour. Demo is repeated with a green circle, and contour/no contour presentation is counterbalanced.

Demo 2: Welsh Castell Coch illusion- based on the Spanish castle illusion (Sadowski, undated).

After adaptation to a chromatically inverse picture of Castell Coch, an achromatic photo of the same castle appears in full (illusory) colour. However, we have modified this to also

present the achromatic photo upside down, which greatly reduces the intensity of the afterimage. This demonstrates that although consistent contexts can enhance afterimage visibility, inconsistent contexts act in an opposing manner and suppress the afterimage (Daw, 1962).

Photo of castle Coch reproduced with permission from PS Photographic (http://www.psphotographic.co.uk/).

Demo 3: Afterimage illusion by van Lier et al., 2009.

Pink and green star shapes are adapted equally, yet afterimage visibility of these two stars is dependent on which of the afterimages is surrounded by a luminance outline.

This video has been reproduced from Current Biology, 19(8), van Lier, Vergeer and Antis, Filling-in afterimage colors between the lines, R323-R324.

Demo 4: Real stimulus version of the illusion by van Lier et al., 2009

We have modified the van Lier et al., (2009) illusion by substituting the afterimages for real, faint, blurry chromatic stars. The real stimulus version is less compelling than the original afterimage version because the star outside the contour is more likely to be perceived (especially after initial viewing before fading mechanisms occur). This is consistent with our data showing that afterimages are more modulated by contextual edges than are real stimuli.

Demo 5: Afterimage jellies (afterimages filling-in an expanding and contracting contour)

We created this novel, dynamic, illusion, by placing a shrinking and growing contour around a checkerboard of afterimages. This results in the perception that the afterimages are shrinking and growing with the contours (See Figure A.4). Thus, despite the adaptation regions remaining either larger or smaller than the contours at almost every point, we perceive the afterimages wobbling in size with the contour oscillations. This illusion demonstrates that afterimages fill-in and fill-out dynamically to stick to contour edges. We

have intensified the effect by displaying a checkerboard of different coloured afterimages, all wobbling at different phases.

(a) Adapt – 3s
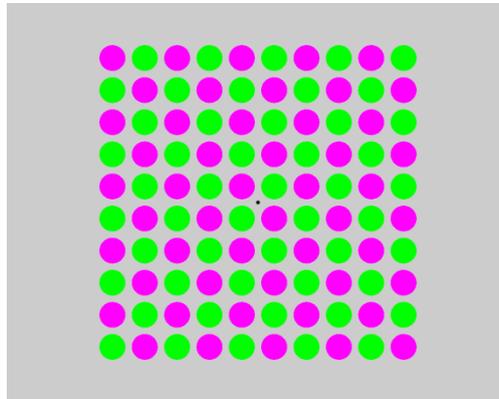
(b) Physical oscillations on the screen (smooth modulation in contour size)
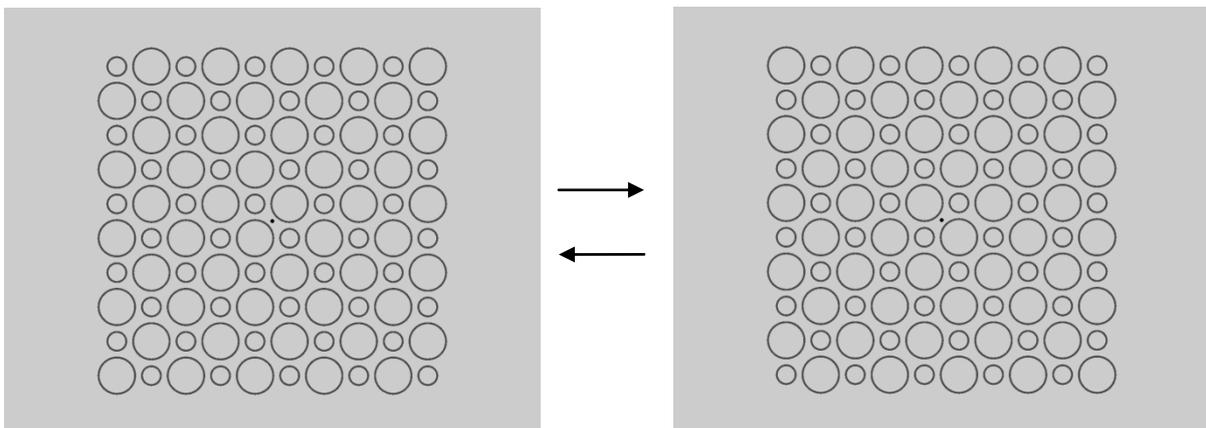
(c) Perceptual oscillations of afterimages (smooth modulation in afterimage size).
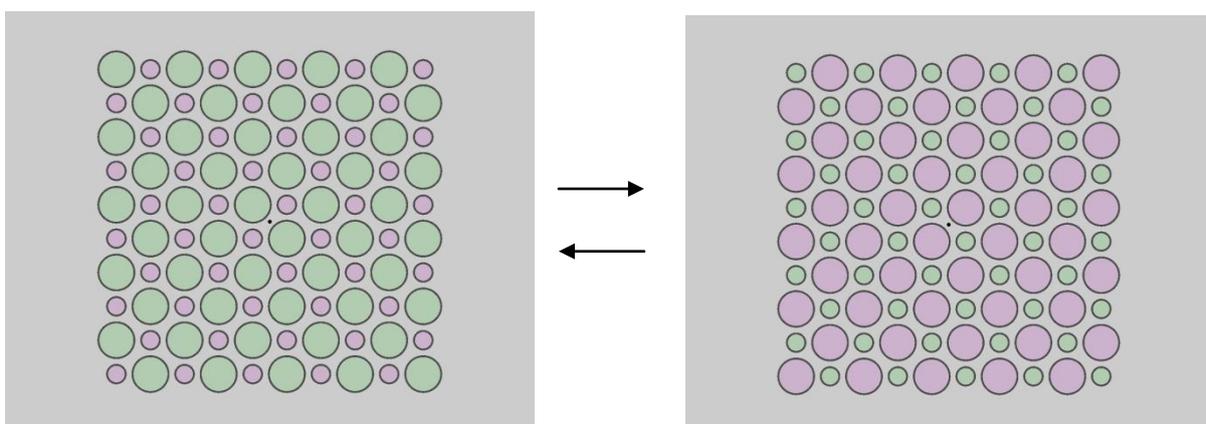
Figure A.4. Screen shots of the afterimage jellies illusion. (a) Observers adapt to pink and green circles to generate a colour afterimage. (b) Physically, black outlines of the circles smoothly shrink and grow (oscillate in size). (c) Perceptually, afterimages shrink and grow inside the black outlines. This is remarkable because on the retina, the adaptation areas of the circles are all the same size, yet of conscious perception of them is dependent on contour size.

References

Abramov, I., Gordon, J., & Chan, H. (1991). Color appearance in the peripheral retina: effects of stimulus size. *Journal of the Optical Society of America, 8*(2), 404-414.

Aristotle, Ross, W. D., & Smith, J. A. (1910). *The works of Aristotle* (Vol. 3). Oxford: Clarendon Press.

Bachmann, T., & Murd, C. (2010). Covert spatial attention in search for the location of a color-afterimage patch speeds up its decay from awareness: Introducing a method useful for the study of neural correlates of visual awareness. *Vision Research, 50*(11), 1048-1053.

Baijal, S., & Srinivasan, N. (2009). Types of attention matter for awareness: A study with color afterimages. *Consciousness and Cognition, 18*(4), 1039-1048.

Barlow, H. B., & Sparrock, J. M. B. (1964). The Role of Afterimages in Dark Adaptation. *Science, 144*(3624), 1309-1314.

Barnes, J., Howard, R. J., Senior, C., Brammer, M., Bullmore, E. T., Simmons, A., et al. (1999). The functional anatomy of the McCollough contingent colour after-effect. *NeuroReport, 10*(1), 195-199.

Beer, D., Wortman, J., Horwitz, G., & MacLeod, D. (2005). Compensation of white for macular filtering. *Journal of Vision, 5*(8), 282.

Bell, C. (1823). On the motions of the eye, in illustration of the uses of the muscles and nerves of the orbit. *Philosophical Transactions of the Royal Society of London, 113*, 166-186.

Belmore, S. C., & Shevell, S. K. (2008). Very-long-term chromatic adaptation: Test of gain theory and a new method. *Visual neuroscience, 25*(03), 411-414.

Bergamin, O., Bizzarri, S., & Straumann, D. (2002). Ocular torsion during voluntary blinks in humans. *Investigative ophthalmology & visual science, 43*(11), 3438-3443.

Blake, R., Fox, R., & McIntyre, C. (1971). Stochastic properties of stabilized-image binocular rivalry alternations. *Journal of Experimental Psychology, 88*(3), 327.

Blake, R., & Hirsch, H. V. (1975). Deficits in binocular depth perception in cats after alternating monocular deprivation. *Science, 190*(4219), 1114-1116.

Blakemore, C., & Cooper, G. F. (1970). Development of the Brain depends on the Visual Environment. *Nature, 228*(5270), 477-478.

Bloj, M. G., Kersten, D., & Hurlbert, A. C. (1999). Perception of three-dimensional shape influences colour perception through mutual illumination. *Nature, 402*(6764), 877-879.

Bodis-Wollner, I., Bucher, S. F., & Seelos, K. C. (1999). Cortical activation patterns during voluntary blinks and voluntary saccades. *Neurology, 53*(8), 1800-1800.

Bolte, S., Holtmann, M., Poustka, F., Scheurich, A., & Schmidt, L. (2007). Gestalt perception and local-global processing in high-functioning autism. *Journal of Autism and Developmental Disorders, 37*(8), 1493-1504.

Bompas, A., & O'Regan, J. K. (2006a). Evidence for a role of action in colour perception. *Perception, 35*(1), 65-78.

Bompas, A., & O'Regan, J. K. (2006b). More evidence for sensorimotor adaptation in color perception. *Journal of Vision, 6*(2), 145-153.

Bompas, A., Powell, G., & Sumner, P. (2013). Systematic biases in adult color perception persist despite lifelong information sufficient to calibrate them. *Journal of Vision, 13*(1), 1-19.

Bompas, A., & Sumner, P. (2008). Sensory sluggishness dissociates saccadic, manual, and perceptual responses: An S-cone study. *Journal of Vision, 8*(8), 1-13.

Bone, R. A., Landrum, J. T., & Cains, A. (1992). Optical density spectra of the macular pigmentin vivo andin vitro. *Vision Research, 32*(1), 105-110.

Bone, R. A., Landrum, J. T., Fernandez, L., & Tarsis, S. L. (1988). Analysis of the macular pigment by HPLC: retinal distribution and age study. *Investigative Ophthalmology & Visual Science, 29*(6), 843-849.

Bour, L. J., Aramideh, M., & Ongerboer De Visser, B. W. (2000). Neurophysiological Aspects of Eye and Eyelid Movements During Blinking in Humans. *Journal of Neurophysiology, 83*(1), 166-176.

Bour, L. J., de Visser, B. O., Aramideh, M., & Speelman, J. (2002). Origin of eye and eyelid movements during blinking. *Movement Disorders, 17*(2), 30-32.

Boynton, R. M., Schafer, W., & Neun, M. E. (1964). Hue-Wavelength Relation Measured by Color-Naming Method for Three Retinal Locations. *Science, 146*(3644), 666-668.

Brainard, D. H., Roorda, A., Yamauchi, Y., Calderone, J. B., Metha, A., Neitz, M., et al. (2000). Functional consequences of the relative numbers of L and M cones. *Journal of the Optical Society of America, 17*(3), 607-614.

Brenner, E., & Cornelissen, F. W. (2005). A way of selectively degrading colour constancy demonstrates the experience dependence of colour vision. *Current Biology, 15*(21), R864-866.

Brewster, D. (1826). On the optical illusion of the conversion of cameos into intaglios and of intaglios into cameos, with an account of other analogous phenomena. *Edinburgh Journal of Science, 4*, 99-108.

Brindley, G. S. (1959). The discrimination of after-images. *Journal of Physiology, 147*(1), 194-203.

Brindley, G. S. (1962). Two new properties of foveal after-images and a photochemical hypothesis to explain them. *The Journal of Physiology, 164*(1), 168-179.

Bristow, D., Haynes, J.-D., Sylvester, R., Frith, C. D., & Rees, G. (2005). Blinking Suppresses the Neural Response to Unchanging Retinal Stimulation. *Current Biology, 15*(14), 1296-1300.

Burr, D. C. (2005). Vision: In the Blink of an Eye. *Current Biology, 15*(14), R554-R556.

Burr, D. C., Morrone, M. C., & Ross, J. (1994). Selective suppression of the magnocellular visual pathway during saccadic eye movements. *Nature, 371*(6497), 511-513.

Carpenter, R. H. S. (1972). After-images on backgrounds of different luminance: a new phenomenon and a hypothesis. *The Journal of Physiology, 226*(3), 713-724.

Chan, D., Crutch, S., & Warrington, E. (2001). A disorder of colour perception associated with abnormal colour after-images: a defect of the primary visual cortex. *Journal of Neurology, Neurosurgery & Psychiatry, 71*(4), 515-517.

Chaparro, A., Stromeyer Iii, C. F., Kronauer, R. E., & Eskew Jr, R. T. (1994). Separable red-green and luminance detectors for small flashes. *Vision Research, 34*(6), 751-762.

Chen, S.-F., Chang, Y., & Wu, J.-C. (2001). The spatial distribution of macular pigment in humans. *Current Eye Research, 23*(6), 422-434.

Clark, J. J., & O'Regan, J. K. (2000, 2000). *A temporal-difference model of perceptual stability in color vision.* Paper presented at the 15th International Conference on Pattern Recognition.

Clifford, C. W. G., & Rhodes, G. (2005). *Fitting the mind to the world: Adaptation and after-effects in high-level vision* (Vol. 2): Oxford University Press, USA.

Cole, G. R., Stromeyer III, C. F., & Kronauer, R. E. (1990). Visual interactions with luminance and chromatic stimuli. *Journal of the Optical Society of America, 7*(1), 128-140.

Collewijn, H., van der Steen, J., & Steinman, R. M. (1985). Human eye movements associated with blinks and prolonged eyelid closure. *Journal of Neurophysiology, 54*(1), 11-27.

Coren, S., & Porac, C. (1974). The fading of stabilized images: Eye movements and information processing. *Perception & Psychophysics, 16*(3), 529-534.

Craik, K. J. W. (1940). Origin of Visual After-images. *Nature, 145*(3674), 1.

Creed, R. S., & Graniy, R. (1928). On the latency of negative after-images following stimulation of different areas of the retina. *Journal of Physiology, 66*(3), 281-298.

Cuijpers, R. H., Kappers, A. M. L., & Koenderink, J. J. (2003). The metrics of visual and haptic space based on parallelity judgements. *Journal of Mathematical Psychology, 47*(3), 278-291.

Curcio, C. A., Allen, K. A., Sloan, K. R., Lerea, C. L., Hurley, J. B., Klock, I. B., et al. (1991). Distribution and morphology of human cone photoreceptors stained with anti-blue opsin. *The Journal of Comparative Neurology, 312*(4), 610-624.

Cynader, M., & Chernenko, G. (1976). Abolition of direction selectivity in the visual cortex of the cat. *Science, 193*(4252), 504-505.

Dakin, S., & Frith, U. (2005). Vagaries of visual perception in autism. *Neuron, 48*(3), 497.

Danilova, M. V., & Mollon, J. D. (2006). The comparison of spatially separated colours. *Vision Research, 46*(6), 823-836.

Darwin, R. W., & Darwin, E. (1786). New Experiments on the Ocular Spectra of Light and Colours. By Robert Waring Darwin, M. D.; Communicated by Erasmus Darwin, M. D. F. R. S. *Philosophical Transactions of the Royal Society of London, 76*, 313-348.

Daw, N. W. (1962). Why After-Images are not Seen in Normal Circumstances. *Nature, 196*(4860), 1143-1145.

Delahunt, P. B., Webster, M. A., Ma, L., & Werner, J. S. (2004). Long-term renormalization of chromatic mechanisms following cataract surgery. *Visual neuroscience, 21*(3), 301-308.

Dodwell, P. C., & Humphrey, G. K. (1990). A functional theory of the McCollough effect. *Psychological Review, 97*(1), 78.

Eisner, A., & Enoch, J. (1982). Some effects of 1 week's monocular exposure to long-wavelength stimuli. *Perception & Psychophysics, 31*(2), 169-174.

Ekroll, V. r., & Faul, F. (2012). Basic characteristics of simultaneous color contrast revisited. *Psychological Science, 23*(10), 1246-1255.

Emmert, E. (1881). Grössenverhältnisse der nachbilder. *Klinische Monatsblätter für Augenheilkunde, 19*, 443-450.

Ernst, M. O., & Banks, M. S. (2002). Humans integrate visual and haptic information in a statistically optimal fashion. *Nature, 415*(6870), 429-433.

Ernst, M. O., & Bülthoff, H. H. (2004). Merging the senses into a robust percept. *Trends in Cognitive Sciences, 8*(4), 162-169.

Eskew Jr, R. T., Stromeyer Iii, C. F., & Kronauer, R. E. (1994). The time-course of chromatic facilitation by luminance contours. *Vision Research, 34*(23), 3139-3144.

Evinger, C., Shaw, M. D., Peck, C. K., Manning, K. A., & Baker, R. (1984). Blinking and associated eye movements in humans, guinea pigs, and rabbits. *Journal of Neurophysiology, 52*(2), 323-339.

Exner, S. (1890). Das verschwinden der nachbilder bei augenbewegungen. *Zeitschrift fur Psychologie und Physiologie der Sinnesorgane, 1*, 47-51.

Fairchild, M. D., & Reniff, L. (1995). Time course of chromatic adaptation for color-appearance judgments. *Journal of the Optical Society of America, 12*(5), 824-833.

Farnsworth, D. (1943). The Farnsworth-Munsell 100-Hue and Dichotomous Tests for Color Vision. *Journal of the Optical Society of America, 33*(10), 568-574.

Farnsworth, D. (1949). *The Farnsworth-Munsell 100 hue test for the examination of color discrimination: manual.* Baltimore: Munsell Color Company.

Feitosa-Santana, C., D'Antona, A. D., & Shevell, S. K. (2012). What kinds of contours bound the reach of filled-in color? *Journal of Vision, 11*(2), 1-11.

Felsen, G., & Dan, Y. (2005). A natural approach to studying vision. *Nature Neuroscience, 8*(12), 1643-1646.

Ferree, C. E. (1908). The Intermittence of Minimal Visual Sensations. Studied from the Side of the Negative After-Image. I. The Fluctuation of the Negative After-Image. *The American Journal of Psychology, 19*(1), 58-129.

Ferree, C. E., & Rand, G. (1919). Chromatic thresholds of sensation from center to periphery of the retina and their bearing on color theory: Part I. *Psychological Review, 26*(1), 16-41.

Ferster, D., & Miller, K. D. (2000). Neural Mechanisms of Orientation Selectivity in the Visual Cortex. *Annual Review of Neuroscience, 23*(1), 441-471.

Field, D. J. (1987). Relations between the statistics of natural images and the response properties of cortical cells. *Journal of the Optical Society of America, 4*(12), 2379-2394.

Fine, I., MacLeod, D. I. A., & Boynton, G. M. (2003). Surface segmentation based on the luminance and color statistics of natural scenes. *Journal of the Optical Society of America, 20*(7), 1283-1291.

Fiorentini, A., & Mazzantini, L. (1965). Inhibition of after-images due to voluntary eye movements. *Atti della Fondazione Giorgio Ronchi, 20*(3), 307-320.

Flynn, J. T. (2003). Adler's physiology of the eye: Clinical application, 10th ed. *Archives of Ophthalmology, 121*(11), 1667-1667.

Forde, J., & Mackinnon, G. E. (1975). Binocular stimulation and the fragmentation of after-images. *The Quarterly Journal of Experimental Psychology, 27*(4), 565-577.

Foster, D. H. (2011). Color constancy. *Vision Research, 51*(7), 674-700.

Franz, S. I. (1899). After-images. *The Psychological Review: Monograph Supplements, 3*(2), i.

Freeman, T. C. A. (2007). Extra-Retinal Vision: Firing at Will. *Current Biology, 17*(3), R99-R101.

Friedman, A. H., & Marchese, A. L. (1978). Positive after-image, PAI: Early erasure by saccadic eye movement or Jendrassik manoeuvre. *Cellular and Molecular Life Sciences, 34*(1), 71-73.

Friedman, S. H., Zhou, H., & von der Heydt, R. (2003). The coding of uniform colour figures in monkey visual cortex. *The Journal of Physiology, 548*(2), 593-613.

Frisby, J. P. (1980). *Seeing: Illusion, brain and mind*: Oxford University Press Oxford.

Gandhi, N. J., & Katnani, H. A. (2011). Interactions of eye and eyelid movements. *The Oxford Handbook of Eye Movements*, 323.

Geisler, W. S. (2008). Visual perception and the statistical properties of natural scenes. *Annual Review of Psychology, 59*(1), 167-192.

Gerling, J. r., & Spillmann, L. (1987). Duration of visual afterimages on modulated backgrounds: Postreceptoral processes. *Vision Research, 27*(4), 521-527.

Gerrits, H. J. M., Erning, L. J. T. O., & Eijkman, E. G. J. (1988). Afterimages: a collective term for percepts of different origin. *Experimental Brain Research, 72*(2), 279-286.

Ginsborg, B. L. (1952). Rotation of the Eyes during Involuntary Blinking. *Nature, 169*(4297), 412-413.

Ginsborg, B. L., & Maurice, D. M. (1959). Involuntary movements of the eye during fixation and blinking. *The British journal of ophthalmology, 43*(7), 435.

Gordon, J., & Abramov, I. (1977). Color vision in the peripheral retina. II. Hue and saturation. *Journal of the Optical Society of America, 67*(2), 202-207.

Gori, M., Del Viva, M., Sandini, G., & Burr, D. C. (2008). Young children do not integrate visual and haptic form information. *Current Biology, 18*(9), 694-698.

Gowdy, P. D., StromeyerIii, C. F., & Kronauer, R. E. (1999). Facilitation between the luminance and red-green detection mechanisms: enhancing contrast differences across edges. *Vision Research, 39*(24), 4098-4112.

Gregory, A. H., & Arnold, P. (1971). Fragmentation and closure in after-images. *Vision Research, 11*(12), 1473-1477.

Gregory, R. L. (1997). Knowledge in perception and illusion. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences, 352*(1358), 1121-1127.

Grüsser, O. J., Krizic̦, A., & Weiss, L. R. (1987). Afterimage movement during saccades in the dark. *Vision Research, 27*(2), 215-226.

Gur, M., & Akri, V. (1992). Isoluminant stimuli may not expose the full contribution of color to visual functioning: Spatial contrast sensitivity measurements indicate interaction between color and luminance processing. *Vision Research, 32*(7), 1253-1262.

Hammond, B. R., Johnson, E. J., Russell, R. M., Krinsky, N. I., Yeum, K.-J., Edwards, R. B., et al. (1997). Dietary modification of human macular pigment density. *Investigative ophthalmology & visual science, 38*(9), 1795-1801.

Hansen, T., & Gegenfurtner, K. R. (2009). Independence of color and luminance edges in natural scenes. *Visual neuroscience, 26*(01), 35-49.

Hansen, T., Pracejus, L., & Gegenfurtner, K. R. (2009). Color perception in the intermediate periphery of the visual field. *Journal of Vision, 9*(4).

Hayhoe, M. M., & Williams, D. R. (1984). Disappearance of afterimages at 'impossible' locations in space. *Perception, 13*(4), 455-459.

Helmholtz, H. (1962). *Helmholtz's Treatise on Phyiological Optics* (Vol. II). New York: Dover Publications, Inc.

Heywood, S., & Churcher, J. (1971). Eye movements and the afterimage—I. Tracking the afterimage. *Vision Research, 11*(10), 1163-1168.

Hibino, H. (1992). Red-green and yellow-blue opponent-color responses as a function of retinal eccentricity. *Vision Research, 32*(10), 1955-1964.

Hilz, R. L., & Cavonius, C. R. (1970). Wavelength Discrimination Measured with Square-Wave Gratings. *Journal of the Optical Society of America, 60*(2), 273-277.

Hilz, R. L., Huppmann, G., & Cavonius, C. R. (1974). Influence of luminance contrast on hue discrimination. *Journal of the Optical Society of America, 64*(6), 763-766.

Hogervorst, M. A., & Eagle, R. A. (1998). Biases in three-dimensional structure-from-motion arise from noise in the early visual system. *Proceedings of the Royal Society of London. Series B: Biological Sciences, 265*(1406), 1587-1593.

Horwitz, G. D., Chichilnisky, E. J., & Albright, T. D. (2005). Blue-Yellow Signals Are Enhanced by Spatiotemporal Luminance Contrast in Macaque V1. *Journal of Neurophysiology, 93*(4), 2263-2278.

Ibbotson, M. R., & Cloherty, S. L. (2009). Visual Perception: Saccadic Omission: Suppression or Temporal Masking? *Current Biology, 19*(12), R493-R496.

Iwasaki, M., Kellinghaus, C., Alexopoulos, A. V., Burgess, R. C., Kumar, A. N., Han, Y. H., et al. (2005). Effects of eyelid closure, blinks, and eye movements on the electroencephalogram. *Clinical Neurophysiology, 116*(4), 878-885.

Jameson, D., Hurvich, L. M., & Varner, F. D. (1979). Receptoral and postreceptoral visual processes in recovery from chromatic adaptation. *Proceedings of the National Academy of Sciences, 76*(6), 3034-3038.

Jazayeri, M., & Movshon, J. A. (2006). Optimal representation of sensory information by neural populations. *Nature Neuroscience, 9*(5), 690-696.

Jones, P. D., & Holding, D. H. (1975). Extremely long-term persistence of the McCollough effect. *Journal of experimental psychology. Human perception and performance, 1*(4), 323.

Kaufman, P., Alm, A., & Adler, F. (2003). *Adler's physiology of the eye: clinical application.* St Louis, MO: CV.

Kelly, D. H., & Martinez-Uriegas, E. (1993). Measurements of chromatic and achromatic afterimages. *Journal of the Optical Society of America, 10*(1), 29-37.

Kennard, D. W., Hartmann, R. W., Kraft, D. P., & Boshes, B. (1970). Perceptual suppression of afterimages. *Vision Research, 10*(7), 575-585.

Kingdom, F. A. A. (2008). Perceiving light versus material. *Vision Research, 48*(20), 2090-2105.

Komatsu, H., Kinoshita, M., & Murakami, I. (2002). Neural responses in the primary visual cortex of the monkey during perceptual filling-in at the blind spot. *Neuroscience research, 44*(3), 231-236.

Kourkoulou, A., Kuhn, G., Findlay, J. M., & Leekam, S. R. (2013). Eye Movement Difficulties in Autism Spectrum Disorder: Implications for Implicit Contextual Learning. *Autism Research*.

Lee, R. J., & Smithson, H. E. (2012). Context-dependent judgments of color that might allow color constancy in scenes with multiple regions of illumination. *Journal of the Optical Society of America, 29*(2), A247-A257.

Leigh, R. J., Newman, S. A., Folstein, S. E., Lasker, A. G., & Jensen, B. A. (1983). Abnormal ocular motor control in Huntington's disease. *Neurology, 33*(10), 1268-1268.

Leigh, R. J., & Zee, D. S. (1999). *The Neurology of Eye Movements*. New York: Oxford University Press.

Loomis, J. M. (1972). The photopigment bleaching hypothesis of complementary after-images: A psychophysical test. *Vision Research, 12*(10), 1587-1594.

Lotto, R. B. (2011). http://www.lottolab.org/illusiondemos/Demo%2014.html.

Lou, L. (2001). Effects of voluntary attention on structured afterimages. *Perception, 30*(12), 1439-1448.

Lou, L. (2007). Apparent afterimage size, Emmert's law, and oculomotor adjustment. *Perception, 36*(8), 1214.

MacKinnon, G. E., Forde, J., & Piggins, D. J. (1969). Stabilized images, steadily fixated figures, and prolonged after-images. *Canadian Journal of Psychology/Revue canadienne de psychologie, 23*(3), 184.

MacLeod, D. I., & Boynton, R. M. (1979). Chromaticity diagram showing cone excitation by stimuli of equal luminance. *Journal of the Optical Society of America, 69*(8), 1183-1186.

Magnussen, S., Spillmann, L., Stürzel, F., & Werner, J. S. (2004). Unveiling the foveal blue scotoma through an afterimage. *Vision Research, 44*(4), 377-383.

Magnussen, S., & Torjussen, T. (1974). Sustained visual afterimages. *Vision Research, 14*(8), 743-744.

Mahroo, O. A. R., & Lamb, T. D. (2004). Recovery of the human photopic electroretinogram after bleaching exposures: estimation of pigment regeneration kinetics. *The Journal of Physiology, 554*(2), 417-437.

Matin, E. (1974). Saccadic suppression: A review and an analysis. *Psychological Bulletin, 81*(12), 899-917.

Matteson, H. H. (1965). After-images observed with intermittent background illumination. *Vision Research, 5*(4-5), 123-132.

Maunsell, J. H., & Gibson, J. R. (1992). Visual response latencies in striate cortex of the macaque monkey. *Journal of Neurophysiology, 68*(4), 1332-1344.

McCollough, C. (1965). Color adaptation of edge-detectors in the human visual system. *Science, 149*(3688), 1115-1116.

McDougall, W. (1901). Some new observations in support of Thomas Young's Theory of Light and colour visionI (III. Conclusion). *Mind, X*(1), 347-382.

McKeefry, D. J., Murray, I. J., & Parry, N. R. A. (2007). Perceived shifts in saturation and hue of chromatic stimuli in the near peripheral retina. *Journal of the Optical Society of America, 24*(10), 3168-3179.

McKeefry, D. J., Parry, N. R. A., Murray, I. J., & Panorgias, A. (2008). The perception of chromatic stimuli in the peripheral human retina. *Psichologija, 38*, 19-28.

McLelland, D., Ahmed, B., & Bair, W. (2009). Responses to Static Visual Images in Macaque Lateral Geniculate Nucleus: Implications for Adaptation, Negative Afterimages, and Visual Fading. *Journal of Neuroscience, 29*(28), 8996-9001.

McLelland, D., Baker, P. M., Ahmed, B., & Bair, W. (2010). Neuronal Responses during and after the Presentation of Static Visual Stimuli in Macaque Primary Visual Cortex. *Journal of Neuroscience, 30*(38), 12619-12631.

Melcher, D. (2007). Predictive remapping of visual features precedes saccadic eye movements. *Nature Neuroscience, 10*(7), 903-907.

Merriam, E. P., Genovese, C. R., & Colby, C. L. (2007). Remapping in Human Visual Cortex. *Journal of Neurophysiology, 97*(2), 1738-1755.

Mollon, J. D. (1974). After-effects and the brain. *New Scientist, 61*, 479-482.

Mollon, J. D. (1995). *Seeing color*. Cambridge: Cambridge University Press.

Montag, E. D. (1997). Influence of boundary information on the perception of color. *Journal of the Optical Society of America, 14*(5), 997-1006.

Morrone, M. C., Ross, J., & Burr, D. (2005). Saccadic eye movements cause compression of time as well as space. *Nature Neuroscience, 8*(7), 950-954.

Mullen, K. T., & Kingdom, F. A. (2002). Differential distributions of red-green and blue-yellow cone opponency across the visual field. *Visual neuroscience, 19*(1), 109-118.

Mullen, K. T., & Losada, M. A. (1994). Evidence for separate pathways for color and luminance detection mechanisms. *Journal of the Optical Society of America, 11*(12), 3136-3151.

Mullen, K. T., Sakurai, M., & Chu, W. (2005). Does L/M cone opponency disappear in human periphery? *Perception, 34*(8), 951-959.

Murgatroyd, H., & Bembridge, J. (2008). Intraocular pressure. *Continuing Education in Anaesthesia, Critical Care & Pain, 8*(3), 100-103.

Murray, I. J., Parry, N. R. A., & McKeefry, D. J. (2006). Cone opponency in the near peripheral retina. *Visual neuroscience, 23*, 503-507.

Murray, I. J., Parry, N. R. A., McKeefry, D. J., Valberg, A., & Panorgias, A. Sex-related differences in peripheral human color vision: A color matching study. *Journal of Vision, 12*(1), 1-10.

Nakamura, K., & Colby, C. L. (2002). Updating of the visual representation in monkey striate and extrastriate cortex during saccades. *Proceedings of the National Academy of Sciences of the United States of America, 99*(6), 4026-4031.

Neitz, J., Carroll, J., Yamauchi, Y., Neitz, M., & Williams, D. R. (2002). Color Perception Is Mediated by a Plastic Neural Mechanism that Is Adjustable in Adults. *Neuron, 35*(4), 783-792.

Nerger, J. L., Volbrecht, V. J., & Ayde, C. J. (1995). Unique hue judgments as a function of test size in the fovea and at 20-deg temporal eccentricity. *Journal of the Optical Society of America A: Optics, Image Science, and Vision, 12*(6), 1225-1232.

Nickerson, D., & Granville, W. C. (1940). Hue Sensibility to Dominant Wave-Length Change and the Relation Between Saturation and Colorimetric Purity. *Journal of the Optical Society of America, 30*(4), 159-162.

Nowak, L. G., Munk, M. H. J., Girard, P., & Bullier, J. (1995). Visual latencies in areas V1 and V2 of the macaque monkey. *Visual neuroscience, 12*(02), 371-384.

O'Regan, J. K., & Noe, A. (2001). A sensorimotor account of vision and visual consciousness. *Behavioral and Brain Sciences, 24*(5), 939-972.

Otte, T., Valberg, A., & Spillmann, L. (2006). Surround-induced foveal afterimage pulsation: Evidence for a long-range neural effect. *Vision Research, 46*(8-9), 1187-1193.

Owen, D. H., & Chalfant, C. (1970). Central integration effects with stabilized afterimages. *Attention, Perception, & Psychophysics, 7*(5), 284-286.

Parry, N. R. A., McKeefry, D. J., & Murray, I. J. (2006). Variant and invariant color perception in the near peripheral retina. *Journal of the Optical Society of America, 23*(7), 1586-1597.

Parry, N. R. A., Panorgias, A., McKeefry, D. J., & Murray, I. J. (2012). Real-world stimuli show perceived hue shifts in the peripheral visual field. *Journal of the Optical Society of America, 29*(2), A96-A101.

Pellicano, E., & Burr, D. C. (2012). When the world becomes too real: A Bayesian explanation of autistic perception. *Trends in Cognitive Sciences, 16*(10), 504-510.

Pinna, B., Brelstaff, G., & Spillmann, L. (2001). Surface color from boundaries: a new 'watercolor' illusion. *Vision Research, 41*(20), 2669-2676.

Purves, D., & Lotto, R. B. (2011). *Why we see what we do redux: A wholly empirical theory of vision*: Sinauer Associates.

Ramachandran, V. S. (1988). Perception of shape from shading. *Nature, 331*(6152), 163-166.

Richters, D. P., & Eskew, R. T., Jr. (2009). Quantifying the effect of natural and arbitrary sensorimotor contingencies on chromatic judgments. *Journal of Vision, 9*(4), 27 21-11.

Ridder III, W. H., & Tomlinson, A. (1993). Suppression of contrast sensitivity during eyelid blinks. *Vision Research, 33*(13), 1795-1802.

Ridder III, W. H., & Tomlinson, A. (1997). A comparison of saccadic and blink suppression in normal observers. *Vision Research, 37*(22), 3171-3179.

Riggs, L. A., Kelly, J. P., Manning, K. A., & Moore, R. K. (1987). Blink-related eye movements. *Investigative ophthalmology & visual science, 28*(2), 334-342.

Rinner, O., & Gegenfurtner, K. R. (2000). Time course of chromatic adaptation for color appearance and discrimination. *Vision Research, 40*(14), 1813-1826.

Robertson, V. M., & Fry, G. A. (1937). After-images observed in complete darkness. *The American Journal of Psychology, 49*(2), 265-276.

Ross, J., & Ma-Wyatt, A. (2004). Saccades actively maintain perceptual continuity. *Nature Neuroscience, 7*(1), 65-69.

Ross, J., Morrone, M. C., & Burr, D. C. (1997). Compression of visual space before saccades. *Nature, 386*(6625), 598-601.

Ross, J., Morrone, M. C., Goldberg, M. E., & Burr, D. C. (2001). Changes in visual perception at the time of saccades. *Trends in Neurosciences, 24*(2), 113-121.

Sadowski, J. http://www.johnsadowski.com/big_spanish_castle.php.   Retrieved 5 August, 2011

Schefrin, B. E., & Werner, J. S. (1990). Loci of spectral unique hues throughout the life span. *Journal of the Optical Society of America, 7*(2), 305-311.

Schmolesky, M. T., Wang, Y., Hanes, D. P., Thompson, K. G., Leutgeb, S., Schall, J. D., et al. (1998). Signal Timing Across the Macaque Visual System. *Journal of Neurophysiology, 79*(6), 3272-3278.

Schutz, A. C., Braun, D. I., Kerzel, D., & Gegenfurtner, K. R. (2008). Improved visual sensitivity during smooth pursuit eye movements. *Nature Neuroscience, 11*(10), 1211-1216.

Scott, A. B., & Collins, C. C. (1973). Division of labor in human extraocular muscle. *Archives of Ophthalmology, 90*(4), 319.

Shevell, s., K, St Clair, R., & Hong, S. W. (2008). Misbinding of color to form in afterimages. *Visual neuroscience, 25*(03), 355-360.

Shimojo, S., Kamitani, Y., & Nishida, S. (2001). Afterimage of perceptually filled-in surface. *Science, 293*(5535), 1677-1680.

Simoncelli, E. P., & Olshausen, B. A. (2001). Natural image statistics and neural representation. *Annual Review of Neuroscience, 24*(1), 1193-1216.

Simons, D. J. (2000). Attentional capture and inattentional blindness. *Trends in Cognitive Sciences, 4*(4), 147-155.

Simons, D. J., & Chabris, C. F. (1999). Gorillas in our midst: Sustained inattentional blindness for dynamic events. *Perception-London, 28*(9), 1059-1074.

Simons, D. J., & Rensink, R. A. (2005). Change blindness: past, present, and future. *Trends in Cognitive Sciences, 9*(1), 16-20.

Smith, T., & Guild, J. (1931). The C.I.E. colorimetric standards and their use. *Transactions of the Optical Society, 33*(3), 73.

Smithson, H., & Zaidi, Q. (2004). Colour constancy in context: Roles for local adaptation and levels of reference. *Journal of Vision, 4*(9), 693-710.

Sommerburg, O., Keunen, J. E. E., Bird, A. C., & van Kuijk, F. J. G. M. (1998). Fruits and vegetables that are sources for lutein and zeaxanthin: the macular pigment in human eyes. *British Journal of Ophthalmology, 82*(8), 907-910.

Sperandio, I., Chouinard, P. A., & Goodale, M. A. (2012). Retinotopic activity in V1 reflects the perceived and not the retinal size of an afterimage. *Nature Neuroscience, 15*(4), 540-542.

Stabell, B., & Stabell, U. L. F. (1996). Peripheral Colour Vision: Effects of Rod Intrusion at Different Eccentricities. *Vision Research, 36*(21), 3407-3414.

Stevenson, S. B., Volkmann, F. C., Kelly, J. P., & Riggs, L. A. (1986). Dependence of visual suppression on the amplitudes of saccades and blinks. *Vision Research, 26*(11), 1815-1824.

Stringham, J. M., & Hammond, B. R. (2007). Compensation for light loss due to filtering by macular pigment: relation to hue cancellation. *Ophthalmic and Physiological Optics, 27*, 232-237.

Stringham, J. M., Hammond, B. R., Wooten, B. R., & Snodderly, D. M. (2006). Compensation for Light Loss Resulting From Filtering by Macular Pigment: Relation to the S-Cone Pathway. *Optometry & Vision Science, 83*(12), 887-894

Sugita, Y. (2004). Experience in Early Infancy Is Indispensable for Color Perception. *Current Biology, 14*(14), 1267-1271.

Suzuki, S., & Grabowecky, M. (2003). Attention During Adaptation Weakens Negative Afterimages. *Journal of Experimental Psychology: Human Perception and Performance, 29*(4), 793-807.

Taya, R., & Ohinata, S. (2002). Afterimage oscillation after a brief light flash. *Japanese Psychological Research, 44*(2), 99-106.

Theeuwes, J., & Lucassen, M. P. (1993). An adaptation-induced pop-out in visual search. *Vision Research, 33*(16), 2353-2357.

Thompson, P., & Burr, D. C. (2009). Visual aftereffects. *Current Biology, 19*(1), R11-R14.

Tolias, A. S., Moore, T., Smirnakis, S. M., Tehovnik, E. J., Siapas, A. G., & Schiller, P. H. (2001). Eye Movements Modulate Visual Receptive Fields of V4 Neurons. *Neuron, 29*(3), 757-767.

Trezona, P. W. (1960). The after-effects of a white light stimulus. *The Journal of Physiology, 150*(1), 67-78.

Troland, L. T. (1917). Preliminary note: The influence of changes of illumination upon after-images. *The American Journal of Psychology, 28*(4), 497-503.

Tsuchiya, N., & Koch, C. (2005). Continuous flash suppression reduces negative afterimages. *Nature Neuroscience, 8*(8), 1096-1101.

Tulunay-Keesey, Ã. (1982). Fading of stabilized retinal images. *Journal of the Optical Society of America, 72*(4), 440-447.

Uchikawa, K., & Sato, M. (1995). Saccadic suppression of achromatic and chromatic responses measured by increment-threshold spectral sensitivity. *Journal of the Optical Society of America, 12*(4), 661-666.

van Boxtel, J. J. A., & Koch, C. (2009). Afterimage duration and its modulation by attention and consciousness. *Journal of Vision, 9*(8), 121.

van Boxtel, J. J. A., & Koch, C. (2010). Boundary information and filling-in in afterimage perception. *Journal of Vision, 10*(7), 1159.

van Lier, R., Vergeer, M., & Anstis, S. (2009). Filling-in afterimage colors between the lines. *Current Biology, 19*(8), R323-R324.

Vienot, F. (1983). Color-match changes between the Fovea and the Perifo-vea. *Color Research & Application, 8*, 215-220.

Virsu, V., & Laurinen, P. (1977). Long-lasting afterimages caused by neural adaptation. *Vision Research, 17*(7), 853-860.

Volkmann, F. C. (1962). Vision during Voluntary Saccadic Eye Movements. *Journal of the Optical Society of America, 52*(5), 571-577.

Volkmann, F. C., Riggs, L. A., Ellicott, A. G., & Moore, R. K. (1982). Measurements of visual suppression during opening, closing and blinking of the eyes. *Vision Research, 22*(8), 991-996.

von der Heydt, R., Friedman, S. H., & Zhou, H. (2003). Searching for the neural mechanisms of color filling-in. In L. Pessoa & P. De Weerd (Eds.), *Filling-in: From Perceptual Completion to Cortical Reorganization* (pp. 106-127). Oxford: Oxford University Press.

von Goethe, J. W., & Eastlake, C. L. (1840). *Goethe's Theory of Colours: Translated from the German*: Murray.

von Kries, J. (1970). Contribution to the physiology of visual sensations. In D. MacAdam (Ed.), *Sources of colour science*. Cambridge, MA: MIT Press.

Vul, E., Krizay, E., & MacLeod, D. I. A. (2008). The McCollough effect reflects permanent and transient adaptation in early visual cortex. *Journal of Vision, 8*(12), 1-12.

Wade, N. J. (1974). The effect of orientation in binocular contour rivalry of real images and afterimages. *Perception & Psychophysics, 15*(2), 227-232.

Wade, N. J. (1978). Why do patterned afterimages fluctuate in visibility? *Psychological Bulletin, 85*(2), 338-352.

Wade, N. J. (2000). *A natural history of vision*. Cambridge, MA: MIT Press.

Wang, M., Munch, I. C., Hasler, P. W., Prünte, C., & Larsen, M. (2008). Central serous chorioretinopathy. *Acta ophthalmologica, 86*(2), 126-145.

Washburn, M. F. (1900). The Color Changes of the White Light After-Image, Central and Peripheral. *Psychological Review, 7*(1), 39.

Weale, R. A. (1953). Colour vision in the peripheral retina. *British Medical Bulliten, 9*(1), 55-60.

Webster, M. A. (2011). Adaptation and visual coding. *Journal of Vision, 11*(5).

Webster, M. A., Halen, K., Meyers, A. J., Winkler, P., & Werner, J. S. (2010). Colour appearance and compensation in the near periphery. *Proceedings of the Royal Society B: Biological Sciences, 277*(1689), 1817-1825.

Webster, M. A., & Leonard, D. (2008). Adaptation and perceptual norms in color vision. *Journal of the Optical Society of America, 25*(11), 2817-2825.

Weiskrantz, L. (2002). Prime-sight and blindsight. *Consciousness and Cognition, 11*(4), 568-581.

Weiss, Y., Simoncelli, E. P., & Adelson, E. H. (2002). Motion illusions as optimal percepts. *Nature Neuroscience, 5*(6), 598-604.

Weitzman, D. O., & Kinney, J. A. S. (1969). Effect of Stimulus Size, Duration, and Retinal Location upon the Appearance of Color. *Journal of the Optical Society of America, 59*(5), 640-643.

Werner, J. S., Bieber, M. L., & Schefrin, B. E. (2000). Senescence of foveal and parafoveal cone sensitivities and their relations to macular pigment density. *J. Opt. Soc. Am. A, 17*(11), 1918-1932.

Werner, J. S., & Schefrin, B. E. (1993). Loci of achromatic points throughout the life span. *Journal of the Optical Society of America, 10*(7), 1509-1516.

Wiesel, T. N., & Hubel, D. H. (1965). Comparison of the effects of unilateral and bilateral eye closure on cortical unit responses in kittens. *Journal of Neurophysiology, 28*(6), 1029-1040.

William Yund, E., & Armington, J. C. (1975). Color and brightness contrast effects as a function of spatial variables. *Vision Research, 15*(8), 917-929.

Wilson, M. H., & Brocklebank, R. W. (1955). Complementary hues of after-images. *Journal of the Optical Society of America, 45*(4), 293-299.

Wittenberg, M., Bremmer, F., & Wachtler, T. (2008). Perceptual evidence for saccadic updating of color stimuli. *Journal of Vision, 8*(14), 1-9.

Wolfe, U., Maloney, L. T., & Tam, M. (2005). Distortions of perceived length in the frontoparallel plane: Tests of perspective theories. *Perception & Psychophysics, 67*(6), 967-979.

Worthey, J. A., & Brill, M. H. (1986). Heuristic analysis of von Kries color constancy. *Journal of the Optical Society of America, 3*(10), 1708-1712.

Wuerger, S. (2013). Colour Constancy Across the Life Span: Evidence for Compensatory Mechanisms. *PloS one, 8*(5), e63921 63921-63929.

Wyatt, H. J. (1998). Detecting saccades with jerk. *Vision Research, 38*(14), 2147-2153.

Yarbus, A. (1967). *Eye movements and vision*. New York: Plenum Press.

Yeh, T., Lee, B. B., & Kremers, J. (1996). The time course of adaptation in macaque retinal ganglion cells. *Vision Research, 36*(7), 913-931.

Zaidi, Q., Ennis, R., Cao, D., & Lee, B. (2012). Neural Locus of Color Afterimages. *Current biology : CB, 22*(3), 220-224.

Zee, D. S., Chu, F. C., Leigh, R. J., Savino, P. J., Schatz, N. J., Reingold, D. B., et al. (1983). Blinkâ€¢ saccade synkinesis. *Neurology, 33*(9), 1233-1233.

Zhou, C., & Mel, B. W. (2008). Cue combination and color edge detection in natural scenes. *Journal of Vision, 8*(4), 1-25.