THE CONTRIBUTION OF COLOUR TO VISUAL PROCESSING

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Abstract

The contribution that colour provides in visual object recognition was assessed in a variety of human and non-human primate species. A stimulus was designed to assess the degree to which removal of stimulus chromaticity affected object recognition ability. Stimuli were designed so that all chromatic modulation, all red-green chromatic modulation, all blue-yellow chromatic modulation or all achromatic modulation was removed.

The stimuli were used in tests of object recognition to assess the functional advantage that stimulus colour or stimulus colour mediated by one of the chromatically opponent pathways provided towards object discrimination. Tests were carried out on normal human observers, macaque monkeys (Macca mulatta) and dichromatic marmoset monkeys (Callithrix jacchus). Experiments were conducted to examine the underlying neuronal processing of feature-like stimuli in visual area 1 (V1) of the anesthetised marmoset. Stimuli contained both chromatic and achromatic modulation or only achromatic modulation.

Results showed that for all species, removal of stimulus chromaticity affected object recognition ability. For human observers and the macaque monkeys, the removal of red-green chromatic modulation impaired ability, the removal of blue-yellow chromatic information did not. Although cells were found in marmoset V1 that displayed selectivity for the feature-like elements used to construct the objects used in behavioural tests, they were rare. Few cells showed a significant response when stimuli contained chromaticity.

It was concluded that stimulus chromaticity provides a functional advantage towards the sensory aspects of object recognition in humans, macaques and marmosets. For trichromatic species, there was a bias towards the red-green chromaticity providing a functional advantage. Although few cells were found to link the neural processes in V1 to these findings, V1 remains a candidate in the distributed map of neuro-anatomical areas that have been implicated in combining chromatic and achromatic cues to represent the visual world.

Chapter 1 INTRODUCTION

For normal human and non-human primates the visual modality is the predominant source of information relating about the external environment. Rough estimates of the relative numbers of neural receptors devoted to each of the senses shows how large a contribution vision makes to our understanding of the environment. There are 5-6 million cones and 120-140 million rods present in the human retina (Osterberg, 1935). This compares with 40,000 hair cells in the cochlea (Moller, 2000), 500,000 taste receptors on the tongue (Boron and Boulpaep, 2003), 12 million olfactory receptors in the nose (Shier et al., 2004) and 17,000 tactile receptors in the hand (Carlson, 2001).

I wanted to know how the colour of the light reflected or emitted by an object contributed to the way in which human and non-human primates responded to the kind of objects that are found in the natural environment. Researchers disagree in the extent to which the visual system utilises variations in colour to inform visual behaviour, and I wanted to measure how the chromatic content of objects influenced visually guided behaviour.

1.1 WHY VISION AND VISUAL RECOGNITION ARE IMPORTANT

Vision, visual recognition and visual memory are of huge importance to a wide range of species. These processes aid vertebrates in navigating the environment, reproducing, identifying food, identifying predators, avoiding dangerous situations and recognising beneficial situations (for example a safe habitat in which to reside). When vision fails, animals can be impaired in their ability to survive and reproduce; therefore, vision is an important evolutionary force. In humans the loss of visual ability can have

profound effects on the way that people carry out their day to day activities, and can impede people on a number of levels.

In America, approximately 14 million (1 in 20) people are classified as having low vision (a visual impairment that cannot be corrected by standard glasses or contact lenses) (Pascolini et al., 2004). More than 22 billion US dollars are spent annually on care and services for low vision patients. The number of people effected by low vision is expected to rise dramatically over the next 30 years (National-Alliance-for-Eye-and-Vision-Research, 1995). As such a high percentage of the population is effected by a sight disorder at some point during their life, an understanding of the mechanisms underlying vision are of importance in the development of more efficient and effective ways to manage, prevent or curve sight disorders. It must also be noted that low visual ability affects patients on a number of levels as without the ability to process visual input, visual recognition, identification classification and navigation abilities are affected.

Fundamental research into the neuronal and behavioural mechanisms underlying vision and visual memory in human and non-human primates is essential if applied research is to produce innovative ways to efficiently address the problem of disorders of the visual system.

1.2 COLOUR-BLIND OBSERVERS AND HOW THEY INFORM THEORIES OF VISUAL PROCESSING

A subset of low vision patients have a very specific disorder relating to the inability to discriminate part of the chromatic spectrum that is available to people with

normal visual ability. Colour blind observers generally do not lack all chromatic ability, but will have (for example) an inability to discriminate red from green (Dalton, 1798).

10% of males are affected by colour blindness. This percentage can be slightly higher or lower depending on ethnic background or geographical location. The most common form of colour blindness is red-green colour blindness and is known to be caused by a missing or abnormal long wave cone type (Protanopia or Protanomaly) or a missing or abnormal medium wave cone type (Deutreranopia or Deuteranomaly). Blue-Yellow colour blindness is slightly more rare and results from a missing or abnormal S cone mosaic (tritanopia). Loss of two or more functioning cone types leads to monochromacy where no colour discrimination is possible (although this is very rare).

The study and understanding of the way in which colour blind subjects view and interact with the visual world is important for several reasons. In some sections of specific industries, colour blindness is seen as a limitation to ability (the armed forces for example). If colour-blind subjects can compensate for their reduced chromatic ability (with or without some form of aid) then employers and employees can benefit. The understanding of how missing a cone type effects visual ability is of additional theoretical interest and it is this issue that will be addressed in this thesis.

1.3 COMPARATIVE ADVANTAGES OF ACHROMATIC (LUMINANCE) AND CHROMATIC (COLOUR) INFORMATION

In this thesis, I wanted to address the aspects of the visual processing that were grounded in chromatic ability. Several functional benefits have been suggested to be inherent in chromatically developed visual systems. Chromatic information has been

implicated in segmentation, recognition, identification and classification abilities (Fine et al., 2002, Gegenfurtner et al., 1998, Davidoff and Oostergaard, 1988, Ostergaard and Davidoff, 1985).

Given the potential benefits afforded by chromatically enabled vision, a characterisation of the degree to which colour aids visual behaviour is important in the understanding of normal and abnormal visual systems. As the extent to which colour aids the visual process is currently a matter of debate, it remains an essential area of study. If colour plays little or no role in the fundamental aspects of the visual process then the study of colour in order to develop theories of visual processing in normal and abnormal observers is futile.

One of the ways to highlight the potential benefits that colour vision may provide is to compare the functional relevance of the aspects of natural scenes that are based upon achromatic variations and chromatic variations. Although these two concepts are not purely dissociable, many theories of the functional relevance of colour are based upon the additional benefits that colour affords over achromatic information. Hue boundaries often accompany luminance boundaries and so are important in the breaking up of the visual scene (Kingdom, 2003). Chromatic variations within objects can be used as an additional dimension with which to recognise objects, purely achromatic objects are rarely found in the visual environment and many animals have visual systems that are specifically designed to use chromatic cues to recognise the objects that are essential to their existence (for example the interplay between bees and flowers).

1.4 COLOUR CONSTANCY

It has also been suggested that chromaticity is of functional importance as it represents a relatively stable way of deducing the properties of an object. Over the course of natural variations in lighting conditions (excluding twilight and extreme changes in weather), the chromatic content of an object remains relatively constant, varying non-significantly over the time course of a day and over successive days (Hernandez-Andres et al., 2001). When compared with the luminance variations observed within natural objects over the time course of a day (potentially more than a 100 fold change), chromatic cues remain a relatively stable predictor for object identity.

Where chromatic information does vary over the time course of the day (for instance changes in the properties of the lighting conditions), the visual system of many human and non-human primates can reduce variations by considering the ratio of different parts of the chromatic spectrum emitted by an object. This is illustrated by the fact that the perceived colour of an object depends upon the chromatic properties of the objects that surround it (Land, 1977), a phenomena known as colour constancy. Researchers have therefore suggested that this ability is of use in overcoming any variations that are present in the chromatic properties of natural objects (Foster and Nascimento, 1994). Colour constancy has been proposed to be of functional importance to the visual systems in determining the reflective properties of an object.

1.5 EARLY THEORIES OF COLOUR VISION

Early studies of chromatic function in humans revealed important organisation principles concerning how colour was encoded by the visual process. These ideas were

critical in the development of modern theories of colour vision and are of importance in the understanding the potential benefits that chromaticity can afford vision.

Thomas Young is generally credited with suggesting that colour perception is based upon the balance between three primary colours (red, green and blue). Young went on to speculate that the wide range of colours that he could produce using additive colour mixing were based upon three types of photoreceptor in the eye (red, green and blue sensitive photoreceptor) (Young, 1807). This idea was quantified by Herman von Helmholtz and subsequently became known as the Young-Helmholtz theory. The ideas inherent in the Young-Helmhotz were applied by James Clerk Maxwell in the 1850's (Clerk Maxwell, 1855), who deduced colour blind observers were deficient in one of the cone types present in the retina, and produced one of the earliest demonstrations of colour photography.

These very early studies outline two essential concepts in the study of colour vision. Normal human observers utilise cone photoreceptors that show reasonably broad spectral tuning to three types of light (S cone – blue light, L cone – red light, M cone –green light). The balance of activity in these photoreceptors (similar to the mixing of red-green and blue primaries) results in the production of any natural colour.

1.6 THE INFLUENCE OF COLOUR ON PERCEPTION

Since the seminal studies of colour (which can be traced back to the work of Robert Hooke and Sir Isac Newton) much progress has been made in understanding colour. Never the less, questions remain; How does the relative activity in three different types of photoreceptor contribute towards behaviour? What (if any) advantages does

colour vision provide an organism? How is the central nervous system organised to exploit any contribution that colour affords? General theories of colour vision have suggested a multitude of potential advantages.

Evolutionary accounts propose that trichromatic vision arose in order to allow non-human primates to select fruit from foliage (Allen, 1879). Functional accounts suggest that the colour inherent in natural scenes provides both a sensory and cognitive advantage in recognition memory (Gegenfurtner and Rieger, 2000). Morphological accounts have shown separate classes of retinal neurons devoted to specific aspects of chromatic processing (Calkins and Sterling, 1999).

Despite these studies, there remains research that suggests that colour plays a negligible or diminished role in the visual process (Anglin and Levie, 1985). It is for this reason that a study of the contribution that colour has on the visual process is of great importance and it is hoped that this thesis will address some of the questions relating to the function of colour.

1.7 THE CONTRIBUTION OF COLOUR TO THE VISUAL PATHWAY OF HUMANS

Behavioural studies with human subjects have revealed a great deal of information relating to the limits and characteristics of chromatic ability. Perceptually based colour spaces (CIE, 1931), effects of chromatic adaptation (Krauskopf, 1962) and estimates of the ratio of cone types present in the retina (Carroll et al., 2002) are all examples of findings that reveal the fundamental limits of the human visual stream. Based upon the progress made in examining the fundamental stages of the visual

pathway, researchers have begun to examine the characteristics of the way that chromatic information is used at higher levels of the visual stream. Studies have examined the effect that colour has on the encoding and retrieval of complex naturalistic stimuli, such as scene and natural object perception.

The first section of this thesis (Chapter 3 and Chapter 4) is concerned with these types of question. I wanted to examine the effect that stimulus chromaticity had upon peoples ability to recognise objects. If the presence of stimulus chromaticity had little or no effect on visual ability, then it would mean that the visual system was predominantly using achromatic information to recognise objects. If chromatic information did facilitate performance then this would suggest that higher levels of the visual process were using stimulus chromaticity to aid object recognition. Of particular interest was the contribution that colour provided towards the sensory aspects of object recognition abilities. The resolution of this question was an important first stage in assessing the contribution of colour to the visual process.

1.8 THE INFLUENCE OF COLOUR UPON RECOGNITION ABILITY

Early studies of the effect of colour on subject pictorial recognition ability generally converged upon colour facilitating performance (Borges et al., 1977, Homa and Viera, 1988). However another study failed to find an effect (Anglin and Levie, 1985) and since then a degree of debate has arisen concerning whether or not colour facilitates recognition performance. The discrepancy between these studies could reflect the amount of information available within a stimulus or differences in the fundamental visual attributes (e.g. luminance and contrast) of stimuli. Recent studies that have

controlled for these attributes show that subjects display an advantage in the recognition of natural scenes caused by the presence of chromatic information (Wichmann et al., 2002). The role of colour in the recognition of single objects has also caused debate. This is possibly due to the difficulties in differentiating the cognitive and the sensory aspects of any potential benefit that colour may afford. In some studies a clear advantage provided by the chromatic properties of objects has been observed (Lee and Perrett, 2000, Lee and Perrett, 1997). In one study, only if colour was of diagnostic use (it was seen as typical for a particular object) colour was then shown to facilitate recognition (Tanaka and Presnell, 1999). In other studies no chromatically based facilitating effect has been observed (Biederman and Ju, 1988). In the Biederman study, two classes of stimuli were used, full colour photographs of objects and line drawings corresponding to the major components within objects. The subjects' task was to either name or verify (against a target name) presentations of slides containing the different types of objects. The authors also examined whether the colour diagnosticity of the objects that were presented aided performance. Based upon the lack of any effects relating to the removal of surface colour, the authors concluded that colour, brightness and texture only provide a secondary cue in the recognition of objects.

1.9 THE CONTRIBUTION OF DIFFERENT TYPES OF COLOUR TOWARDS VISUAL PROCESSING

As well as examining the general role of colour in the visual process some studies have also examined the role of specific parts of the chromatic spectrum. Normal humans (like old world monkeys) utilise two chromatically opponent pathways in visual perception. Signals from the red sensitive or L cones are opposed with signals from the

green sensitive or M cones. This arises in a red-green opponent pathway. Signals from the blue sensitive or S cones are opposed with a combination of signals from the L and M cones. This produces a blue-yellow opponent pathway. Opponent pathways therefore balance the degree to which one cone type is activated versus another cone type (or combination of cone types).

The result of this process is that chromatic information is encoded in an antagonistic fashion. This explains why there are no reddish green hues, as equal combinations of red and green chromaticity nullify the opponent system. Research that has focused upon segregating the effect that chromatic information encoded by the two opponent pathways has found differences in the contribution that they provide in visual perception.

Studies of shape discrimination have shown that thresholds relating to the discrimination of objects encoded by the red-green pathway are lower than thresholds relating to the blue-yellow pathway (Mullen et al., 2000). The nature of the photoreceptor mosaic within the retina also suggests that the resolution afforded by the S cone pathway (blue-yellow) is less than that of the L versus M pathway (red-green). This has been supported by empirical studies (Mullen and Kingdom, 2002). Based upon these findings there is a strong possibility that the different opponent pathways will have different functional roles. It is hoped that the results from the first section (Chapter 3 and Chapter 4) of this thesis will contribute towards an understanding of these functional aspects.

1.10 THE CONTRIBUTION OF COLOUR IN MACAQUES

Historically, macaque monkeys have been used as a model of the fundamental stages of the human visual process. This is because they share many characteristics such as trichromatic vision, similar spectral sensitivities of cone types and chromatically opponent retinal and post retinal processing. One of the advantages of studying macaque visual processing is that invasive measurements and manipulations of the neuronal underpinnings of the visual process can allow a greater understanding of the inherent mechanisms underlying vision.

Over the past 50 years, huge progress has been made in establishing the neuronal properties of the fundamental stages of the macaque visual pathway. Lesion studies and single unit recording have aided researchers in attaching function to structure for many of the anatomical areas in visual cortex (for review of single cell studies see (Lennie, 1998) or (Merigan and Maunsell, 1990, Merigan and Maunsell, 1993, Merigan and Pham, 1998) for lesion studies). Similar lines of psychophysical research as conducted with human observers have revealed the limits of chromatic detection and discrimination in macaques (DeValois et al., 1974, Cowey and Stoerig, 2001). However, as with the human literature few studies have examined the contribution of colour to higher level visual processes such as the recognition of objects. These kind of studies are important as they allow researchers to tie together findings relating to the studies of neural process with findings relating to behavioural processes. In the second section (Chapter 5 and Chapter 6) of this thesis I attempt to address the contribution that colour makes to the behavioural object recognition abilities of macaques. Assessing the nature and type of advantage that colour afforded macaque vision would be of use in relating the visual

abilities of macaques and humans and consequently in relating studies examining neural function with behavioural function.

1.11 THE EVOLUTION OF MACAQUE CHROMATIC ABILITY

As old world monkeys are relatively unique amongst the primate linage because of their trichromatic vision (although some female new world monkeys have the ability as well), questions emerge concerning why and how such an ability emerged. This is of interest as the evolutionary pressures that shaped trichromatic vision could potentially have relevance to the function of human colour vision. Several theories have emerged relating to possible reasons why the trichromatic colour vision, found in old world primates, emerged from the dichromatic colour vision present in new world primates. One body of research suggests that as larger monkeys required fruit to supplement their diet, advanced chromatic discrimination and recognition abilities were required to identify ripe fruit (for a review see (Regan et al., 2001)). Other researchers propose similar ideas relating to the detection of ripe from unripe leaves (Lucas et al., 1998). In both of the above situations colour is being used in diagnostic and sensory contexts, however there have been examples where colour had been used in a purely sensory manner (for example to break camouflage) (Caine et al., 2003). Therefore further study is required to elaborate the precise nature that chromaticity affords the visual process and the advantage that trichromatic vision has over dichromatic vision.

1.12 THE CHROMATIC DISCRIMINATION ABILITIES OF MACAQUES AND HUMANS

Macaque monkeys have chromatic discrimination abilities that are very similar to humans (Loop and Crossman, 2000). Despite the generally convergent results, a few differences have been found between the species. Studies of cone weightings (the ratio of L:M:S cones that contribute to the visual process) have provided different results for humans and macaque monkeys.

In a study where red-green equiluminance points were established using psychophysical (humans) and electrophysiological (macaques) methods, differing ratios were found for each of the species (1:1 LM ratio for macaques) and (2:1 LM ratio for humans) (Dobkins et al., 2000). Differences in the ratio of cone types are also a product of normal human visual systems and therefore may not reflect differences in visual ability.

1.13 MACAQUE OBJECT DISCRIMINATION ABILITY

As well as having similar colour vision abilities as human subjects, macaques show a similar (if not greater) ability to recognise previously viewed colour pictures (Ringo et al., 1986). Macaque monkeys have also shown an ability to learn incredibly subtle discriminations based upon shape, size, orientation and the chromatic properties of objects. Although the limits and characteristics of macaque visual recognition have been extensively studied (especially with reference to supporting anatomical cortical areas), few studies have used controlled naturalistic stimuli in order to assess the contribution that colour makes to this process.

In one study (Delorme et al., 2000) various types of naturalistic stimuli were presented either in colour or in black and white. Monkeys and humans had to detect a target in briefly flashed, novel stimuli. Macaques showed no difference in their ability to recognise object stimuli that did and did not contain chromatic information, however a difference was observed in the monkeys' reaction time. This effect was limited to the detection of food targets. These findings differ from the results found in the human literature showing that within constrained situations colour facilitates recognition ability. Further study is therefore required to confirm the nature and extent to which colour benefits macaque recognition ability.

1.14 THE CONTRIBUTION OF COLOUR IN THE MACAQUE VISUAL STREAM

One of the reasons that it is so important to tie together theories of chromatic processing in humans and macaque monkeys, is that a great deal of knowledge has been obtained relating various anatomical areas within the macaque brain to behavioural function. A number of anatomically distinct structures and cortical areas have been identified and related to various visual functions. The optic nerve (that originates from the retina) projects to the lateral geniculate nucleus (LGN). The LGN is located within the thalamus and has a distinct structure with a number of anatomically segregated layers. Lesions of the parvocellular layers within the LGN lead to a reduction in chromatic contrast sensitivity (Merigan, 1991).

The striate cortex (V1) is located within the occipital lobe. Selective lesions within this area have also been shown to impair chromatic processing (Cowey and Stoerig, 2001), although there is a degree of debate concerning the implication of V1 in

chromatic processing, some authors proposing a modular view of chromatic processing based in V4 (Essen and Zeki, 1978).

Visual areas V2,V3 and V4 reside in extra striate cortex. Of these areas, lesions of V4 are the most effective in producing chromatic deficits (Cowey and Gross, 1970) mainly in the ability to discriminate colour. Inferior temporal cortex (IT) is located within the temporal lobe. Lesions of this area have also been shown to produce deficits in chromatic discrimination (for a review see (Gross, 1992)).

As such a developed understanding has been achieved through the use of the above techniques, why is it of importance to test macaques with a behavioural task to assess the contribution of colour to the visual stream? The traditional view of chromatic processing in the macaque visual process is that visual area V4 is specialised in the representation of the chromatic properties of the image (Essen and Zeki, 1978). Given that this area is reasonably high in the visual stream, many researchers have speculated that the contribution that colour affords the visual process is manifested at a relatively cognitive or abstracted level. This is exemplified by theories of colour aiding the diagnostic properties of objects and theories relating to colour constancy.

This contrasts with humans studies that highlight the contribution of colour at a lower sensory level. I therefore chose to test the sensory contribution that colour provided macaques in the recognition of novel objects. A deficit caused by the removal of chromatic stimulus information would suggest that lower visual areas are critical in chromatic processing, and would provide a greater understanding of the contribution of lower visual areas to the visual process.

1.15 THE CONTRIBUTION OF COLOUR IN MARMOSETS

Marmosets, unlike macaques, are not a predominantly trichromatic species. Male marmosets are all dichromats and female marmosets may be dichromatic or trichromatic (see (Shyue et al., 1998) for further information). One of the potential advantages that marmosets provide is that they can be used to model the type of dichromatic vision observed in colour deficient human observers. As with macaques, the use of marmoset monkeys allows invasive as well as non-invasive measures to be taken relating to the visual process. Similar arguments can therefore be proposed relating to the need to obtain behavioural measures of the extent to which colour contributes to the visual process.

By comparing behavioural and physiological measures it is possible to obtain a comprehensive theory of neural function and in the case of marmosets this can be extended to colour deficient (dichromatic) visual systems. I wanted to know whether the presence of chromaticity within visual objects had a similar effect in dichromatic visual systems as it did in trichromatic visual systems. This had important theoretical and practical implications (Caine and Mundy, 2000).

1.16 THE GENETIC ORIGINS OF THE COMMON MARMOSET

The natural habitat of marmosets is the rainforest canopy between Panama and Brazil. Animals are arboreal and are approximately the size of a large rat. Marmosets are specialised sap and gum eaters but can also eat spiders, insects, lizards, fruit and buds. They are diurnal and tend to range a 0.5 – 1 acre area. Social groups will defend territory using sent markings, calls and aggressive behaviour.

Marmosets differ in their visual ability in comparison with old world monkeys based upon their genetic origins. Genetically, a single X linked locus encodes a middle to long-wave length opsin which is polymorphic in nature. Taken together with the autosomally linked short wave opsin, this leads to a situation where all males and homozygous females are dichromatic. All heterozygous females are trichromats. A single X chromosome linked gene codes for one of three alleles of ML cone, leading to pigments with maximum spectral sensitivities at 543 nm, 556 nm and 563 nm (Travis et al., 1988).

There is a great deal of speculation concerning how the evolutionary transition between dichromatic and trichromatic visual systems occurred. Most theories of the relative advantages of trichromatic vision over dichromatic vision relate to diet. Frugivory, seed dispersal, the breaking of camouflage have all been proposed as critical factors leading to the development of trichromatic vision.

1.17 MARMOSET CHROMATIC ABILITY

Studies have addressed the function of trichromatic vision over dichromatic vision in marmosets in a number of ways. Klix balls are small spherical objects within which a reward can be placed. Caged animals are provided with these objects as a form of environmental enrichment. Caine and colleagues studied the ability of dichromatic and trichromatic marmosets to retrieve rewards from these objects, and found that trichromatic marmosets were advantaged in this respect (Caine and Mundy, 2000).

Modelling studies have also confirmed this advantage by comparing the natural reflectance spectra of real world objects with the different combinations of cone type in

dichromatic and trichromatic animals (Osorio and Vorobyev, 1996, Regan et al., 2001). Again, trichromatic animals appear to be advantaged in the discrimination of a wider variety of edible objects.

1.18 MARMOSETS OBJECT DISCRIMINATION ABILITY

Like macaques, marmosets have been shown to be able to acquire lists of visual object discrimination pairs. Their ability to retain large sets of object discriminations over long delay periods is less than that of macaques. In a comparison of species visual discrimination abilities Easton and colleagues found that the abilities of marmosets were in line with those of rats, when tested on a similar style of maze-based task. In list learning tasks, marmosets generally tend to take a longer period of time to acquire the same number of similar visual discrimination pairs as macaques (Easton et al., 2000).

The advantages of using marmosets to study visual object learning are numerous. marmosets offer the opportunity to test the abilities of dichromatic and trichromatic visual systems in the same species. The neuronal underpinnings of the marmoset visual pathway are becomingly increasingly well understood (Blessing et al., 2004, Silveira et al., 1999, Ghosh et al., 1997). Practically, marmosets have shorter breeding cycles and are more easily housed than macaques.

As with macaques, it is important to characterise behavioural abilities in order to relate these to neuronal function. Few studies have been conducted that provide controlled measures of the various aspects of marmoset visual ability. I therefore wanted to test the behavioural contribution of colour to object recognition in marmosets in a similar way to macaques.

1.19 THE DIFFERENCE BETWEEN DICHROMATIC AND TRICHROMATIC VISION

The comparison of dichromatic and trichromatic visual systems is of relevance to the role of colour in the visual system as it can help reveal the functional differences between the two evolutionary distinct opponent pathways that have been previously detailed. There is a degree of debate concerning the functional advantages that the two opponent subsystems (B-Y and R-G) afford colour vision.

In dichromatic marmosets, all chromatic discrimination is based upon a single opponent pathway comparing the response of S cones to a class of cones with variable peak sensitivity (in the Middle to Long wavelength range). This pathway has been shown to predate the divergence of mammals (Bowmaker, 1998).

The S cone system has been shown to be advantageous to monkeys in the discrimination of the ripeness of fruit (Sumner and Mollon, 2000). The system has also been shown to be sensitive to differences in greens over changes in the natural illuminate (caused by for example changes in weather conditions). Further possible advantageous factors include increased spatial resolution afforded by dichromatic vision compared to trichromatic vision. This has been proposed as being critical to the feeding habits involving the capturing of insects.

In the trichromatic vision found in catarrhine primates (Old World monkeys and apes), a second L-M opponent system exists. Many researchers think that this system evolved to support frugivory behaviours in old world monkeys. Such arguments are supported by experimental data, trichromatic vision can support discrimination of a wider range of fruits and leaves (Regan et al., 2001, Lucas et al., 1998). Such arguments

would place the red-green opponent pathway as advantageous in the recognition of behaviourally important objects.

Questions therefore emerge concerning the relative functionality of the red-green and blue-yellow opponent pathways in the detection and discrimination of real world objects (particularly those related to diet). It is hoped that by testing the contribution of colour within these separate pathways insight can be gained concerning their relative function.

1.20 THE CONTRIBUTION OF COLOUR IN MARMOSET NEURONS.

As previously detailed, the main advantages of investigating the characteristics of visual processing in non-human primates is that corresponding measures of neuronal response can also be taken. Studies have provided a great deal of information relating to the characteristics of neuronal response in the retina, LGN and visual cortex of non-human primates. Particularly relevant to the issues addressed in this thesis is the way in which cells in visual cortex process and respond to object stimuli that contain chromatic variations.

One of the features of the current research into cell response in visual cortex is that the vast majority of studies have used stimuli that are based upon a Fourier approach to characterising cell response to visual stimuli. They therefore use grating based stimuli to classify the way in which cells respond. Although this has proved a very successful way of characterising cell response (all real world stimuli can be described using a Fourier approach), due to inherent complexities it can be hard to relate the

characteristics of these gratings to theories of visual function based upon real world objects. Recent studies have begun to break this trend and cells in V2 have been found that are responsive for stimuli that have particular characteristics (curvature for example see (Hegde and Van Essen, 2000)).

In this thesis I explored the response of single cells in marmoset visual cortex to feature based stimuli of the type that could be found in a naturalistic setting. I did this in order to relate findings concerning the contribution of colour at a behavioural level to the contribution of colour at a physiological level.

1.21 THE PROCESSING OF STUCTURE IN THE NON-HUMAN PRIMATE VISUAL STREAM

The work of Hubel and Wiesel, based in cat and macaque visual cortex, identified cells in V1 that responded preferentially to moving bars or strips of light (Hubel and Wiesel, 1962, Hubel and Wiesel, 1963, Hubel and Wiesel, 1965, Hubel and Wiesel, 1977). Since then a number of techniques in cat, macaque and marmoset V1 have utilised gratings, reverse correlation, and modelling techniques to converge upon a theory of the optimal stimulus profile to drive various classes of V1 cell. Cells have been show to respond selectively for stimuli of optimal position, orientation, length and width, size, drift rate and chromaticity. More recently studies have begun to investigate whether such cells show emergent properties that are selective for more complex feature based stimuli.

Studies have examined the way in which V1 cells respond to plaids, curves, combinations of lines, and Cartesian gratings. Mixed results have been obtained relating

to the selectivity of V1 cells to higher order feature based stimuli, although modelling studies have shown that units of this nature are critical to the visual process, few studies have reported the presence of these cells in V1, and when they have been found they tend to be rare. Because of this focus has turned to other anatomical areas in the search for the feature based stimuli capable of driving cells in a selective fashion. Studies in V2 have reported a number of cells displaying selectivity for these types of stimuli, however the extent to which cells of this nature exist at a more fundamental level (V1) requires further research.

1.22 THE PROCESING OF COLOUR IN THE NON-HUMAN PRIMATE VISUAL STREAM

Early studies in the non-human primate retina and LGN revealed a class of antagonistic neurons that showed an interaction between the different classes of retinal cone types (L, M or S) (De Valois and Jacobs, 1968) Cone opponent cells that originated in the S cones displayed little or no spatial antagonism and are thought to be predominately conveyed along the koniocellular pathway (Casagrande, 1994). Cone opponent cells conveyed along the parvocellular (PC) pathway were found to be red-green opponent and show spatial antagonism (Derrington et al., 1984).

Derrington and colleagues described the optimal response of these cells using a three dimensional space (DKL space). The space consisted of three cardinal directions, each representing a physiologically distinct visual mechanism. The mechanisms were driven by linear summation of the activity of the various cone types in different proportions. The isochromatic or luminance axis represented stimuli that caused changes in activation in all three cone types.

The constant S axis represented stimuli that caused a change in activation in the L and M cones only. This occurred such that the sum of their activation remained constant. Stimuli that plotted along this axis caused changes in the L and M cone activity in an opponent manner. S cone activity remained constant along this axis. The constant LM axis represents stimuli that cause a change in activation in the S cone only. Activity in the L and M cones remained constant (For a review of the relationship between the above directions and mechanism response see (Krauskopf 1999)).

In trichromatic marmosets, PC ganglion cells have been found that show a similar red-green opponency to those that have been found in macaque (Yeh et al., 1995). In a study comparing dichromat and trichromat PC cells, receptive field dimensions were found to be similar, however a slightly higher (30%) contrast sensitivity was observed in dichromat PC cells compared to trichromat PC cells (Solomon et al., 2004)

The contribution of chromatic processing in non-human primate V1 is less clear. Signals from the magnocellular and parvocellular pathways project to separate layers in V1 (for a review (Callaway, 1998) The different classes of chromatic opponent cell observed in the LGN remains until the input layers of V1 (Chatterjee and Callaway, 2003). However there is some degree of debate relating to whether a similar type of segregation remains in and beyond V1.

Cells in macaque V1 generally show a strong modulation in response caused by achromatic modulation or chromatic and achromatic modulation (Johnson et al., 2001). The preferred direction of modulation for chromatically responsive cells in V1 is not necessarily based upon the same R-G and B-Y cardinal axes that define LGN cell

response. Cells have been found that show chromatic tuning between the cardinal directions and can have reasonably narrow chromatic tuning properties (Lennie et al., 1990). Models of the chromatic tuning of V1 cells suggest that they undergo a form of half wave rectification to elaborate certain colour categories (De Valois and De Valois, 1993).

Chromatic processing in marmoset V1 has been less intensively studied. Cells have been shown to provide a differential response for optimally defined achromatic gratings and similar gratings containing the same achromatic modulation superimposed on a chromatic background (Derrington et al., 2002). Visual space has been shown to retinotopically organised in V1 as in the macaque (Rosa et al., 2000).

1.23 RELATING THE RESPONSE OF SINGLE CELLS TO BEHAVIOUR

The relating of studies based upon behavioural and physiological study is an essential part of developing a unified theory of the visual process. By classifying the limits of the behavioural abilities relating to the visual process and then examining how single cells, assemblies of single cells or cortical regions support these behaviours, it should be possible to gain a full understanding of the mechanisms that underlie the visual process. In the context of this thesis, this meant attempting to find a class of cell that displayed tuning characteristics that were dependent upon the presence of colour in object stimuli. As detailed above, these cells have been found in visual area V1 in a variety of species, however to the best of my knowledge no studies have been conducted in the marmoset V1 that address this issue using naturalistic stimuli.

Another reason for studying the properties of cells at the lowest cortical level of the visual pathway (V1) is that traditional theories of chromatic function place anatomical area V4 as being specialised for chromatic functions. This theory is at odds with a range of experimental studies that show that the chromatic properties of stimuli interact with cell response at a number of levels. Assuming that colour does provide an advantage to visual processes, the possibility remains that this advantage is manifest in cell response at the earlier stages of the visual process (e.g. V1) that have been implicated in the representation of shape and form.

1.24 THE AIMS OF THE THESIS

The aim of this thesis was to assess the contribution of colour to object recognition at a behavioural and physiological level in dichromatic and trichromatic subjects. By relating behavioural findings in humans and physiological findings in non-human primates it was also hoped that the theories concerning the functional use of object chromaticity in behaviour could be compared to the way in which V1 neurons responded to feature like stimuli with and without chromatic content.

There has been a degree of debate concerning whether any advantage that colour affords visual recognition is manifest at a sensory or a cognitive level. I aimed to design an experimental paradigm that separated these two factors by testing human subjects' ability to report if previously viewed objects were familiar or unfamiliar after a variable delay period. I wanted to discount any effects relating to the very fundamental chromatic detection mechanisms by designing object stimuli where chromaticity was specified by subjective threshold. This technique has been previously used in studies designed to identify the cardinal directions of colour space (Krauskopf et al., 1982). The first

experimental chapter (Chapter 3) therefore reports the reliability of a novel task to provide measures of recognition ability relating to the need to use low-level sensory information versus higher level cognitive information.

Having designed an appropriate paradigm I wanted to examine if colour had an effect on the visual recognition ability of normal subjects. As previously detailed, the degree to which colour allows subjects to recognise real world objects in a non-diagnostic way is debated. In order to test theories of the effect of stimulus chromaticity on the visual process, I could design stimuli that contrasted subject performance with objects that did and did not contain chromatic information. I could also examine if the removal of chromatic information conveyed by one or other of the chromatically opponent pathways had a selective effect on recognition ability. This was important in order to address functional issues (R-G function versus B-Y function) and to compare behavioural measures with dichromatic subjects. These results are detailed in Chapter 4 . I found that colour did have an effect on the sensory aspect of object recognition and that this was advantage was specific to the red-green opponent pathway.

When I found that colour contributed to human object recognition, I wanted to find out if similar effects were also observed in non-human primates. Such a comparison was important in order to relate physiological responses to behavioural characteristics.

In Chapter 5 , I examined the way in which macaque list learning ability was effected by similar stimulus manipulations detailed in the human experiment. Macaques have been shown to have very similar visual discrimination abilities to humans (in list learning tasks they can exceed human ability), I therefore expected to find (and found) a

similar deficit in ability caused by the removal of chromatic information and red-green chromatic information.

I also wanted to examine the contribution of colour on visual recognition in a dichromatic species. Such a comparison was important as all of the measures relating to single cell response in V1 were taken in marmosets (Chapter 6), and the study of the dichromatic visual process was of theoretical interest.

Based upon the findings in humans and macaques, I was expecting a small or negligible effect of the removal of stimulus chromaticity. Despite the difficulties in training the Marmosets to perform on an equivalent task to the macaques, effects of chromatic subtraction were recorded. This was an un expected finding, however it justifies the use of the species in examining the way that cells in marmoset V1 respond to chromatic content.

The final two chapters examined whether cells existed in marmoset V1 that were selectively modulated by the types of feature found in the naturalistic objects. I also examined whether colour influenced this response. In Chapter 6 I took the most simple constituent element of the object stimuli possible (a single ellipse) and examined if Marmoset V1 cells showed selectivity for the specific types of ellipse, and if the chromatic content of the ellipse had an effect on cell response. In Chapter 7 I started to combine ellipses in two ellipse configurations. I examined if cells showed selectivity for achromatic versions of this stimulus and if the chromatic content of the ellipse affected cell response.

Chapter 2 GENERAL METHODS

Experimental questions

How were the stimuli that were used to assess visual recognition in human and non-human primates created? What procedures were used in order to ensure that the stimuli were adequately and accurately specified?

What methods were used to test the visual recognition abilities of macaque and marmoset monkeys in chapters 5-6?

What protocol was utilised in order to record the response of single cells in visual area 1 (V1) of anesthetised marmoset monkeys (chapters 7&8)?

2.1 INTRODUCTION

In order to assess the contribution of colour to the visual process at differing levels I used a variety of techniques at both behavioural and physiological levels. Experiments were performed using human subjects, macaque monkeys and marmoset monkeys.

In chapters 3 and 4 behavioural tests of human visual object recognition were performed using a serial recognition paradigm. The test (detailed in Chapter 3) allowed the characterisation of human object recognition ability without the need for blocked lists of study and test objects. Subjects viewed a set of single objects, every object appeared twice (separated by a variable temporal gap) and subjects had to indicate whether the object they were viewing was familiar or unfamiliar.

In Chapter 5 and Chapter 6 behavioural tests of macaque and marmoset visual object recognition were performed using a two alternative list learning technique. The test required the animals to indicate a preference for a single object within multiple object pairs. For each object pair one of the objects was constantly rewarded and the other was constantly unrewarded. Objects pairs were repetitively presented until the animal constantly chose the rewarded objects. This paradigm has been used as a standard test of object discrimination ability in human and non human primates and was an ideal choice to allow the assessment of how colour contributes to visual object discrimination.

In Chapter 7 and Chapter 8 , neurophysiological methods were used to record the cell response of neurons in marmoset V1 for stimuli that contained variable levels

and types of chromatic modulation. In order to relate findings obtained using behavioural techniques to the way in which visually responsive neurons conveyed information it was necessary to test cell response using a type of feature based stimuli.

Methods relating to specific stimulus and task parameters are provided within each of the experimental chapters. General information relating to how techniques were applied to the areas of experimental study are provided within this chapter. Details relating to the flower-like stimuli used within Chapters 3,4,5 and 6 are provided in the first section; along with the screen calibration techniques used for stimulus presentation in all of the data chapters. Details relating to the equipment used in the animal behavioural tasks (Chapter 5 and Chapter 6) are provided in the second section of this chapter. The protocol used to measure cell response (Chapter 7 and Chapter 8) is provided in the final section of this chapter.

2.2 STIMULUS GENERATION METHODS.

2.2.1 Screen calibration

In order to ensure that the experimental stimuli were presented using a reliable and controlled specification, it was necessary to characterise the chromatic and luminance output properties of all of the monitors used in each of the experimental studies. Monitors were characterised by obtaining the luminance output characteristics for each of the three CRT phosphors.

The physical definition of luminance is the amount of luminous flux emitted by a unit area of source into a unit solid angle. This is the objective analogue of subjective brightness. In order to obtain a value in cd/m^2 radiometric flux was weighted using the current CIE Photopic Luminous Efficiency Standard. This value was measured in cd/m^2. It was also necessary to measure the spectral properties of the maximum output of the three CRT phosphors. This value was measured in $w/sr/m^2/nm$. Data was collected across the spectrum of 380-780 nm. This allowed the specification of the chromatic output properties of the monitor output.

2.2.2 Equipment and Software

The output characteristics of all screens used within the experiment were measured using a PR-650 spectrometer (Photoresearch US). The spectral data of the output phosphors was recorded and can be found in the appendices section 10.1.1.1 Gamma curves were measured using the same device and are also provided in appendices section 10.1.1.2. For Chapters 3-6 the calibration routines provided in the

psychophysics toolbox of MATLAB were used to provide the framework for obtaining specified screen output (Brainard, 1997).

2.2.3 Calibration Protocol

The first stage of the linearization process involved obtaining the spectral data for the maximum output of the screen phosphors. Gamma curves were also obtained for each CRT phosphor based upon functions that utilised between 10 and 256 points (depending upon the experimental rig). The CIE co-ordinates were calculated for the maximum output of each of the CRT phosphors and gamma functions were fit to the data obtained for the output characteristics of the CRT guns using an extended power function.

Having calculated the gamma functions for the monitors used in the experimental setup, inverse gamma correction functions could be used to produce CLUTS containing linearized luminance output values. These functions had a RMS error of less than 1 %. This was regarded as an acceptable margin of error. These functions could be used to convert RGB values to CIE co-ordinates, cone excitation values or DKL co-ordinates. The accuracy of the calibration routine is provided in appendices section 10.1.1.3

2.2.4 Stimulus generation

The stimuli used within chapters 3-6 were created by the addition of multiple ellipse elements of variable size, aspect ratio, orientation, chromaticity and luminance on a mid grey background. The way in which the ellipse elements were added was constrained so that the resultant object depicted a flower-like object. The routine that I

used to do this is provided in appendices section 10.2.1 and an example of the stimulus set is provided in Figure 2-3.

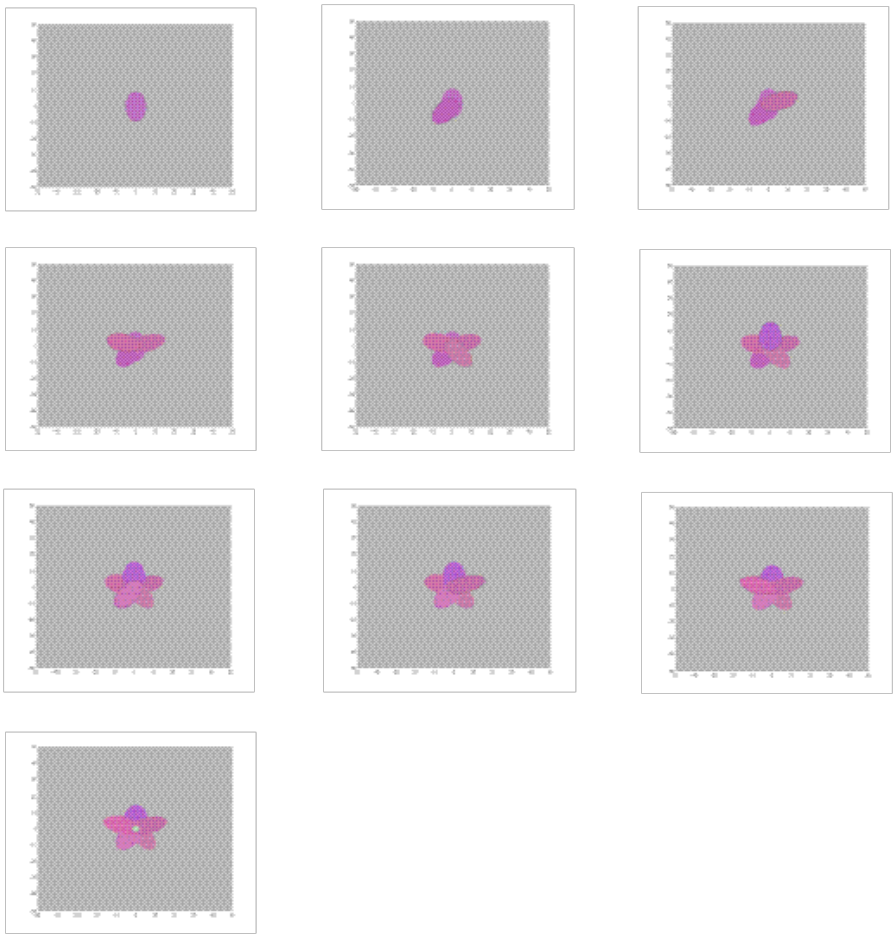

Figure 2-1: Example of the flower-like object generation. Bottom left hand box shows completed object, preceding boxes detail the effect of adding successive ellipses. Colour specification used for illustrative reasons only.

Sets of objects could be created and constrained so that the degree to which the members of the set resembled each other was specified. Objects could also be generated 'on the fly', by providing the routine with a description of the object to be created. This methodology was used so that the object parameters could be generated prior to the

experimental sessions, thus saving processor execution time during the experimental sessions.

The objects were created using the MATLAB routines provided in the appendices section 10.2.1. This was executed using MATLAB version 5.2 (Mathworks UK). The routine accepted arguments that referred to the CLUT (colour look up table) used to shade the object and descriptions of the parameters required to either construct or specify the object.

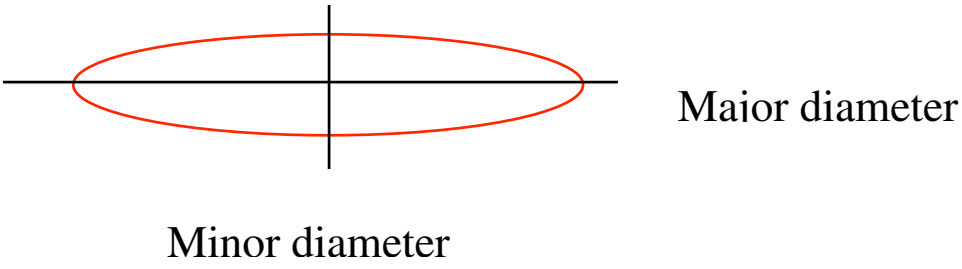

Figure 2-2: Example of ellipse profile.

2.2.5 Stimulus Algorithm

Ellipses were created using the MATLAB patch command. The command plotted a polygon of n points based upon a list of n x and y co-ordinate positions. I used a value of n = 100 in order to trade off between the need for rapid program execution and the visual resolution of the objects. The program created a list of x and y points, these satisfied the general formula for an ellipse (Equation 1). These points were used to plot the outer circumference of the ellipse (the red line in Figure 2-2).

Equation 1

$$x^2/a^2 + y^2/b^2 = 1$$

In order to create a series of discrete points with which to plot the above ellipse it was necessary to calculate values of x and y for a set of angular displacements located around the circumference of the ellipse. In Equation 2, $\theta_{1..360}$ represented a list of 100 equally spaced angles between 0 and 360 degrees.

Equation 2

$$x = a \times \cos\theta_{1..360} - b \times \sin\theta_{1..360}$$
$$y = b \times \sin\theta_{1..360} + a \times \cos\theta_{1..360}$$

It was also necessary to plot ellipses away from the origin. An offset was introduced in order to achieve this. This shifted points in the either the x, y or x and y directions. The focus of the ellipse was moved from the origin to the point defined by the value of the x and y offset (x_o , y_o, Equation 3). This was referred to as the x position and y position of the object stimulus. It was also necessary to rotate ellipses. Ellipses could be rotated about their focus by multiplying the $\cos(\theta_{1..360})$ and $\sin(\theta_{1..360})$ terms in Equation 3 by the sine or cosine of a single angular offset θ. This was referred to as the orientation of the ellipse. Ellipses were also scaled to their appropriate size by multiplying the products of trigonometric terms by a scale factor s (Equation 3). This was referred to as the size of the ellipse.

Equation 3

$$x = a \times \cos\theta_{1..360} \times \cos\theta \times s - b \times \sin\theta_{1..360} \times \sin\theta \times s + x_o$$
$$y = b \times \sin\theta_{1..360} \times \cos\theta \times s + a \times \cos\theta_{1..360} \times \sin\theta \times s + y_o$$

In order to create ellipses of various widths and lengths, it was necessary to control the ratio of the major and minor diameters (the ratio of width to height). This was achieved by varying the aspect ratio of the ellipses that were generated. Equation 4 details the way that the aspect ratio related to the values of a and b detailed previously. By substituting this relationship into the general equation for an ellipse it was possible to specify ellipses by their aspect ratio rather than by the lengths of the major and minor axes.

Equation 4

$$b = 1/\sqrt{r}$$
$$a = 1/b$$

The patch command was therefore supplied with the list of x and y values derived from Equation 3. From these values it produced a 100 sided polygon that approximated an ellipse. A routine was designed so that successive ellipses of varying size, aspect ratio, orientation, hue and luminance could be plotted sequentially. The product of this routine was a montage of ellipses produced in such a way that it resembled a flower-like object. These objects consisted of multiple ellipses plotted around a central point. The objects contained no fewer than 3 ellipses and no more that 35 ellipses. In the middle of the object a circular ellipse was placed this was always rendered so that it was placed on top of the petal-like elements. This flower centre was always positioned in the centre of the screen. Examples of this family of stimuli are shown in Figure 2-3. Using the above techniques, stimulus objects were plotted using the following procedure. A graphical representation of this procedure is shown in Figure 2-1.

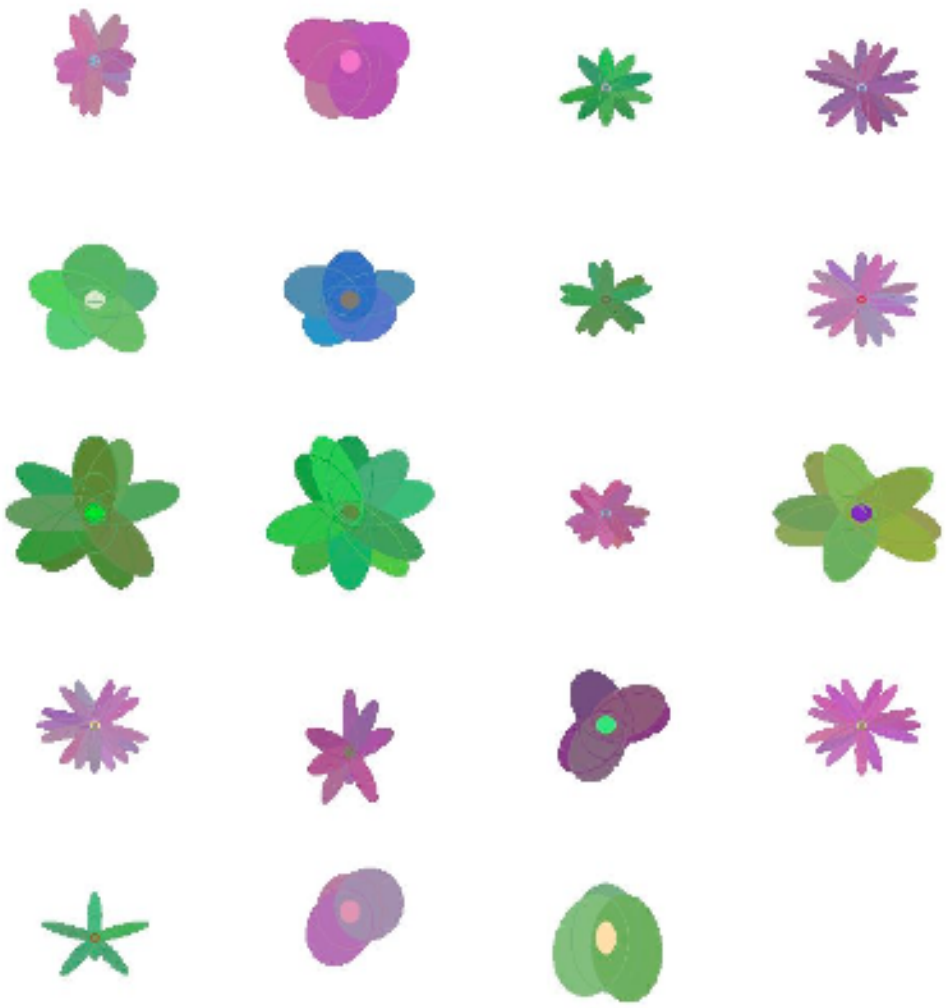

Figure 2-3: Example of flower-like object family. Colours are for illustrative purposes only.

2.2.6 Object generation routine

1) The seed of the random number generator was set to the value of the system clock.

2) The orientation of the first ellipse was set to 90 degrees.

3) A single petal size value was calculated using a probabilistic method. All stimulus petals were set to this size; variations in petal shape were induced using changes in aspect ratio.

4) A general aspect ratio value was calculated using a probabilistic method. This was not used to set the aspect ratio of any part of the stimulus, however it was used to derive the aspect ratio used to shape ellipses (see step 9). This method was used so that consecutive objects varied in their petal shape to a greater degree than the petal shape variations that existed within objects.

5) The number of ellipses within an object was calculated by multiplying the value obtained in step 4 by 7.

6) A grey background box of size 175 by 175 units was produced.

7) A loop was set up that cycled though each ellipse

8) The colour of the ellipse was set by randomly picking a RGB triplet from a list of colours appropriate to the colour specification of the object. The list containing the colours was referred to as a colour lookup table (CLUT).

9) The aspect ratio of the current ellipse was chosen by modulating the value derived in step 4. The value used to perform the modulation was chosen using a probabilistic method.

10) If the ellipse that was being plotted was the last ellipse to be plotted then it was set to be a flower centre. The size and aspect ratio of that ellipse were set to constrained values using the probabilistic method The CLUT index was set to a random value. The focus of the ellipse was positioned in the centre of the screen.

11) The ellipse was calculated and plotted as previously described.

12) The orientation of the next ellipse was derived by selecting a value using a probabilistic method.

13) The x and y position co-ordinates were updated so that the centre of the next ellipse reflected the change in orientation calculated in step 13.

The loop set up in stage 8 was closed.

2.2.7 Colour space

As mentioned in the above techniques, ellipse hue and luminance were calculated by randomly indexing a specific part of a colour lookup table (CLUT). The use of a CLUT was important as it aided fast execution of the program and allowed the specification of the range of colours that was used in all stimuli.

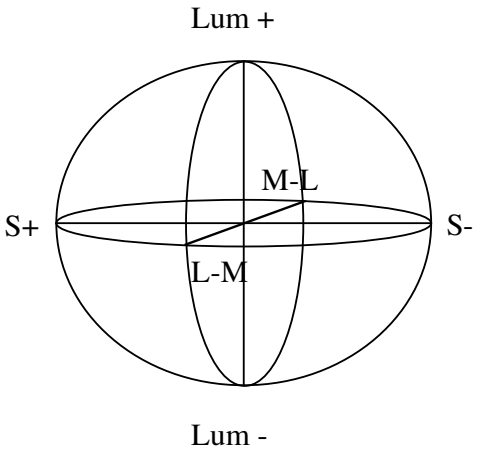

Figure 2-4: Illustration of the DKL sphere

The CLUT was divided into several parts, each of which contained colours that referred to a specific experimental condition. Separate CLUT sections contained RGB values based upon the selective sampling of a constrained part of colour space. In creating the CLUT I chose to use DKL colour space. The DKL space allowed a relationship to be formed between the theoretical physiological mechanisms that underlie the fundamental stages of the visual pathway and the chromatic and luminance specification of the stimulus. Also advantageous was the ability to constrain stimuli so that they only excited a subset of the physiological mechanisms inherent in the DKL model.

DKL space comprises of a 3 dimensional area, in which the response of various visual mechanisms can be represented. This arrangement is shown in Figure 2-4. In previous studies DKL vectors were used to specify the way in which cells in macaque LGN were responsive to stimuli of various chromaticity and luminance (Derrington et al., 1984). In this thesis the space was used to specify stimuli that theoretically isolated one of the opponent mechanisms that arise from the retinal processing of chromatic light (see introduction).

The space consists of three axes, each representing a physiologically distinct visual mechanism that have been previously derived from Derrington and colleagues investigation of the properties of visually responsive neurons in the LGN. The mechanisms are driven by linear summation of the activity of the various cone types in different proportions. The isochromatic or luminance axis represents stimuli that cause changes in activation in all three cone types. Luminance changes cause the three cone types to vary in proportion (relative to their base activity) so the ratio of activity is constant.

The constant S axis represents stimuli that cause a change in activation in the L and M cones only. This occurs such that the sum of their activation remains constant. Stimuli that plot along this axis cause changes in the L and M cones in an opponent manner. S cone activity remains constant along this axis. The constant LM axis represents stimuli that cause a change in activation in the S cone only. Activity in the L and M cones remains constant (For a review of the relationship between the above isolating directions and mechanism response see (Krauskopf 1999)). The mid point of the space where all three axes intersect defines the adaptation point, it is this point about

which our stimuli were modulated (the mid grey background upon which the stimuli were placed).

The values within the CLUT were produced by mapping a vector plotted in DKL space to a device-dependent RGB value (A Judd correction was applied during this process). Vectors were chosen so that the contribution of each DKL mechanism exceeded a theoretical visual threshold, however did not exceed the gamut of the monitor. The contribution of each DKL mechanism was therefore chosen using an un-biased pseudorandom technique. These values were then combined and plotted as a vector as shown in Equation 5.

All vectors originated from the white point of DKL space. For all stimuli that contained luminance variations, vectors were plotted in a direction that negatively modulated the luminance mechanism. By restricting the direction of the DKL vectors to a certain plane of the above colour space, it was also possible to calculate RGB values where the contribution of one of the DKL mechanisms was removed. Specific CLUTS were created for each of these restrictions. Four types of restriction were placed upon the directions that vectors could take

1) No deviations were allowed along the constant S axis.
2) No deviations were allowed along the constant LM axis.
3) No deviations were allowed along the achromatic or luminance axis.
4) No deviations were allowed along either the constant S or constant LM axes.

A CLUT was also generated where no restrictions were placed upon the direction of the DKL vectors.

The following stages were implemented in the generation of each of the CLUTS:

1. A loop was set up. This cycled through every entry within the CLUT

2. Mechanism responses (ΔR_{lum} $\Delta R_{l\text{-}m}$ ΔR_s) (as defined by the routines in the psychophysics toolbox) were assigned for each of the three DKL axes. The values reflected the change in the direction of a mechanism relative to the grey background.

3. The mechanism response values were constrained so that for each mechanism the value was greater than visual threshold, but less than the gamut of the monitor. The contribution of the luminance mechanism was always negative. For reference purposes these values were plotted using the following equation to give an elevation θ and azimuth ϕ for every DKL vector.

Equation 5

$$\phi = \arctan(-\Delta R_s / \Delta R_{l-m})$$
$$\theta = \arctan(\Delta R_{lum} / \sqrt{-\Delta R_s^{\,2} + \Delta R_{l-m}^{\,2}})$$

4. Dependent upon the type of CLUT being produced I set the change in response of one or some of the DKL mechanisms to zero. For 'full colour' CLUTS no manipulations were made to the mechanism responses. For 'minus rg' CLUTS the change in response of the red-green DKL mechanism was set to 0. For 'minus by' CLUTS the change in response of the blue-yellow mechanism was set to 0. For 'minus ch' CLUTS the change in response for both the red-green and blue-yellow mechanisms were set to zero. For 'minus lum' CLUTS the change in response of the luminance mechanism was set to zero.

5. DKL mechanism values were converted into cone increment values ($\Delta P_l\ \Delta P_m\ \Delta P_s$). This was performed using the conversion routine shown in Equation 6.

Equation 6

$$\begin{pmatrix} \Delta P_l \\ \Delta P_m \\ \Delta P_s \end{pmatrix} = \begin{pmatrix} 1.1547 & 1.7889 & 0.0000 \\ 2.3094 & -1.7889 & 0.0000 \\ 1.7321 & 0.0000 & 3.0000 \end{pmatrix} \times \begin{pmatrix} \Delta R_{lum} \\ \Delta R_{l-m} \\ \Delta R_s \end{pmatrix}$$

6. Cone increment values were then converted into absolute cone excitation values ($P_l\ P_m\ P_s$). This was achieved by adding the cone increment values obtained from the previous stage to the cone increment values produced from the stimulus background ($P_{lo}\ P_{mo}\ P_{so}$). This procedure is detailed in Equation 7.

Equation 7

$$\begin{bmatrix} P_l \\ P_m \\ P_s \end{bmatrix} = \begin{bmatrix} \Delta P_l \\ \Delta P_m \\ \Delta P_s \end{bmatrix} + \begin{bmatrix} P_{llo} \\ P_{mo} \\ P_{so} \end{bmatrix}$$

7. Cone excitation values were then converted into CIE XYZ co-ordinates by multiplying by the cone sensitivity estimates of (Smith and Pokorny, 1975) These values are shown in Equation 8.

Equation 8

$$\begin{bmatrix} X \\ Y \\ Z \end{bmatrix} = \begin{bmatrix} P_l \\ P_m \\ P_s \end{bmatrix} \begin{bmatrix} 0.155 & 0.543 & -0.033 \\ -0.155 & 0.457 & 0.033 \\ 0.000 & 0.000 & 0.008 \end{bmatrix}$$

8. CIE XYZ co-ordinates were converted into device specific RGB values via a calibration matrix and gamma correction table.

9. The device specific RGB values were placed into the current CLUT entry

10. The loop started in stage one was closed.

11. The final entry of every CLUT was set to the mid point of the device luminance output. This was used as the stimulus background.

The above routine produced object stimuli depicted in Figure 2-3 The objects were then used in all behavioural tests of recognition ability in chapters 3-6.

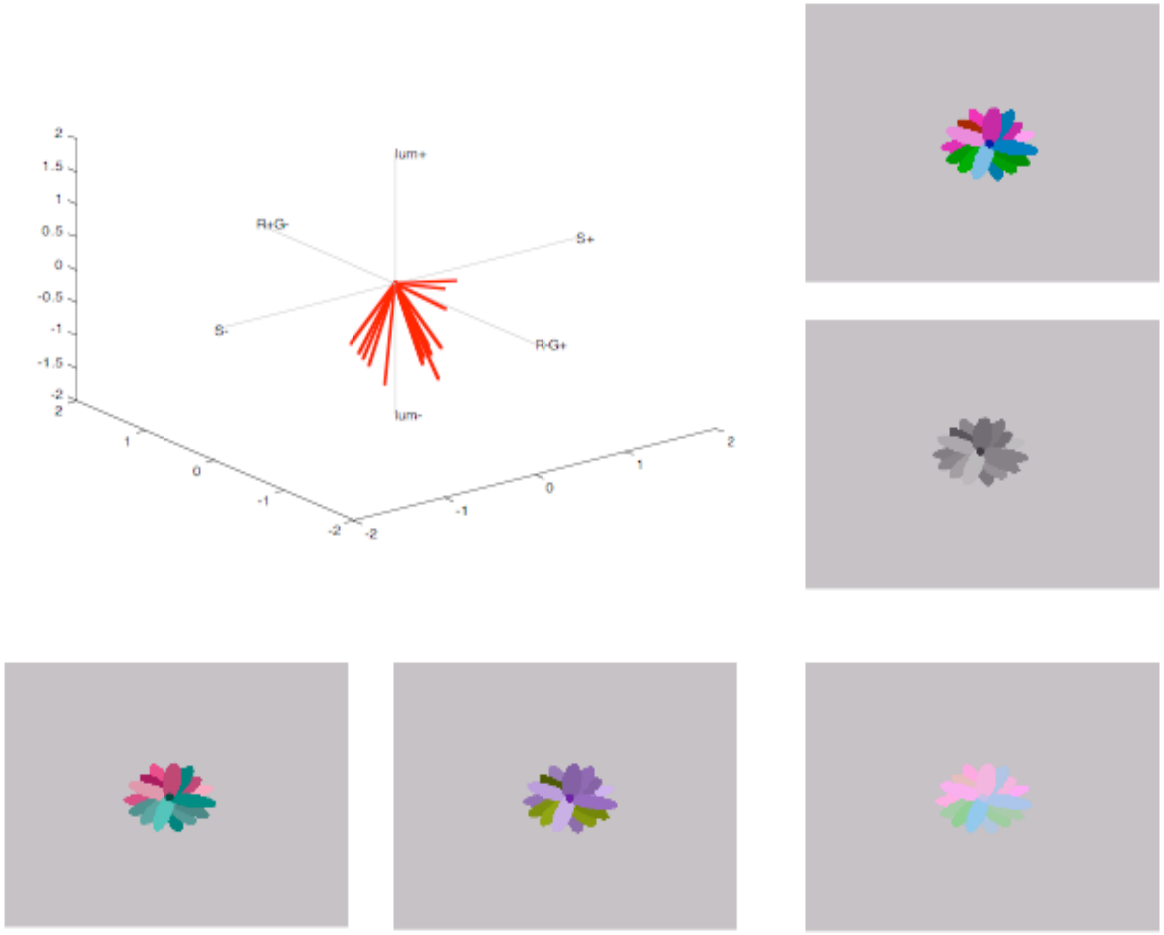

Figure 2-5: Example of the chromatic content of stimuli. Top left hand plot refers to the vectors in DKL space for a full colour object. Figures around the plot refer to the same object rendered in the different colour conditions.

2.3 ANIMAL LEARNING METHODS

2.3.1 Touch Screen methods

2.3.1.1 Introduction

Having used the objects described in the previous section 2.2.4 and depicted in Figure 2-3, to test the object recognition abilities of humans, it was desirable to obtain similar measures for macaques. This would allow comparisons between recognition ability for the different species using the different types of chromatically specified objects. In order to test the visual object discrimination abilities of macaque monkeys, it was necessary to design equipment that could test the monkeys abilities in a controlled and reliable way. The use of automated testing equipment allowed me to get the monkeys to work on list learning tasks without having to interact with the monkey whilst they were working on the task. Before the automated equipment was used the monkeys were pre-trained with a manual Wisconsin box setup (to gain a basic understanding of the task), however all experimental data was collected on an automated test setup. The automated setup used a touchscreen for the monkey to indicate a choice, a computer to display stimuli and collect data and a pellet dispenser to reward the monkey appropriately.

List learning tasks (as opposed to the serial recognition task used with humans) were used as a large body of empirical data has been collected examining the ability of macaques on this type of task. It was also decided that to allow comparison with marmoset behavioural ability a reasonably simple task was required to test ability. Marmosets have never been trained with a delayed match to sample task (DMS)

successfully and the chances of them gaining an ability to perform a serial recognition experiment were slim.

Although it would have been possible to train the macaques on a serial recognition task, the level of abstraction required by the animal would have been much greater than with object reward pairings.

2.3.1.2 Housing

Animals were held in a communal housing area in groups of three. Before the testing session (that commenced between 10.00 am and 11.00 am – prior to the daily feeding) animals were transferred into individual cages and then into a movable transport cage. The animal was then moved from their holding room into a separate testing room. At this point the transport cage was attached either to the Wisconsin box or touch screen equipment. At the end of the testing session the transport cage was moved back to the holding room, the animal was transferred back into their individual cage and then fed.

2.3.1.3 Pretraining

Animals were initially trained using a manual Wisconsin Box setup. The equipment consisted of two reward boxes (65mm by 65mm by 50mm) situated within an aluminium enclosure that had two sliding windows at the front of the equipment and a translucent removable back, behind which the experimenter sat.

When the back of the equipment was in situ and the front windows were open (revealing the reward boxes for the monkey to see), then the experimenter could see the monkey but the monkey could not see the experimenter. The experimenter sat behind the

equipment, closed the front windows (so the monkey could not see inside the equipment), removed the back panel placed the appropriate stimuli in the front of each of the reward boxes and rewarded the box containing the positive stimulus with a small fruit reward. The experimenter then closed the back panel and opened the front window. The monkey was then trained to turn the box containing the reward, take the reward and then wait for the next trial.

Various methods were used to familiarise the monkey with this routine. Naïve monkeys were allowed constant access to the equipment during the training session and small pieces of fruit were scattered around the boxes. These rewards were then placed within the reward boxes, that were turned to face the monkey. Over time the boxes were turned away from the monkey so that the monkey had to turn the box in order to obtain the reward. Stimuli were then placed in the front of the reward boxes and object-reward training commenced.

Animals began with a single discrimination pairs of the type shown in Figure 2-6 and a small number of trials (aprox. 20). This phase of the testing was still regarded as pre training. Over time the number of trials that the animal performed and the number of discrimination pairs that were present within a list was increased. By the end of the Wisconsin box training the animals were performing 50 trials per session on lists of 10 discrimination pairs.

Figure 2-6: Pre-training stimuli (list 4). Title above figure refers to stimulus type: L4 1= list 4, pair 1. + = positive (rewarded) stimulus, - = negative (unrewarded) stimulus.

2.3.1.4 Touch screen equipment

When animals were familiar with the experimental task they were transferred to an automated touch screen setup. The equipment consisted of a 17' Microtouch touch screen (3M UK) and a Med-X (Med-X US) pellet dispenser, interfaced using a standard PC running a Matrox dual head graphics card (Matrox UK). Custom written software in Visual C++ (Microsoft UK) was used to co-ordinate the touch screen response, the reward dispenser and the experimental task. A series of training programs were also written using MATLAB version 6 (Mathworks UK).

The equipment consisted of a steel frame that was bolted to the wall of the testing room. The frame sturdily held the monitor, which was located behind an aluminium façade, designed to only let the monkey touch the screen. An aluminium shelf was located below the screen, this contained a food hopper, into which the 45 mg

banana flavoured reward pellets (Bioserve US) appeared when the animal correctly touched a rewarded object. The pellet dispenser was located above the monitor, pellets were dispensed using a gravity fed system. A IR camera was located above the equipment, this allowed the experimenter (who was located in a separate room) to view the monkey and the food hopper. The monkey worked in a dark room, illuminated by an IR lamp.

Animals were transferred into the automated setup and were initially rewarded by continually dispensing pellets into the food hopper irrespective of their behaviour. Stimuli were then placed onto the screen (pixel co-ordinates 250,250 [left hand object] and 550,250 [right hand object]) and the animals were rewarded (with two 45 mg banana pellets) for touching the screen at any location. The area where a reward was obtained was then shrunk until animals were consistently touching the stimuli, at which point the discrimination learning task commenced. Animals started on a small numbers of trials (20-50) and this was gradually increased until the animals were performing 100+ trials within an experimental session.

2.3.1.5 Experimental Protocol

Irrespective of the length of list or type of equipment used, the protocol for list learning was the same. The monkey had to choose between two objects, placed approximately 8 cm apart. One of the objects in each pair was constantly rewarded and the other object was never rewarded. Upon the monkey indicating (either by touch or turning a box) the correct object stimulus, a reward was provided and the next trial commenced after a short delay (2s for Wisconsin boxes and 1s for the touch screen). If the monkey indicated the wrong object then no reward was provided and a long delay

(5-10s) commenced before the next trial. The experimental session was ended if the monkey refused to work for an extended period of time (> 10 minutes) or if the monkey constantly misbehaved.

2.3.1.6 Randomisation

Wisconsin box testing utilised several Gellerman sequences to randomise the side that the positive stimulus appeared on. Equal numbers of left and right hand positive rewards were contained within each completed session. For lists, equal numbers of each object pair were included in completed sessions. For the touch screen testing, lists were either randomised using a Gellerman sequences or a pseudo random sequence that contained equal number of left and right hand positive stimuli.

2.3.1.7 Screen Calibration

The same process was used to characterise and calibrate the screen as in described in the stimulus generation methods (2.2.1). Details are provided in appendices section 10.1.2.

2.3.2 Y Maze methods

2.3.2.1 Introduction

In order to further compare the effects of chromaticity on recognition ability in different species, marmoset monkeys were also tested on a two choice discrimination task. As with the macaque monkeys, a body of evidence suggests that marmoset monkeys can perform accurately on tests of this nature (see Chapter 6 for references).

It was decided that the best way to implement this paradigm was to allow the marmosets to roam freely within a maze environment. Marmosets display foraging abilities in their natural habitat and it was hoped that their innate abilities would ideally suit such an environment. Stimulus choice was therefore indicated by visiting the arm of the Y maze that contained a version of the rewarded or unrewarded stimulus. Upon visiting the correct arm (that contained a rewarded stimulus) a small piece of marshmallow reward would appear in the floor of the maze.

The Y Maze was used as it provided several advantages over the manual techniques used by previous researchers. Experimenter effects were avoided as the maze could be controlled from an adjacent room. Marmosets could therefore perform the experimental task in a quiet environment free from distraction. The maze also utilised the natural tendency for marmosets to roam around their environment, foraging for food.

2.3.2.2 Pretraining

The animals used within the Y maze were all previously trained using a Wisconsin box setup. Details of this procedure are provided in (Derrington et al., 2002).

2.3.2.3 Transport cages

Animals were housed in communal holding areas. Between two and four animals resided within each cage. To commence the testing session, the experimental animal was moved from its home cage to the maze equipment using a triangular transport cage. The cage was designed so that animals could move easily from the holding cages to the transport cage, and the transport cage could then fit into the central part of the maze. The animal was then free to move between the transport cage and the maze environment.

2.3.2.4 Equipment

The Y maze was used to test the marmosets on a version of the two choice list learning task detailed in the previous section 2.3.1 The maze consisted of three Perspex arms interconnected by a central chamber. A computer monitor was situated at the end of each arm and displayed stimuli so that the animals within the maze could see the stimuli when positioned in the central part of the maze. The marmosets task was to visit the 'start arm' containing a cueing stimulus at which point the two visual objects that formed a discrimination pair would appear on the monitors at the end of the other two arms. Each arm contained detectors that sensed where the marmoset was positioned within the maze and a reward system that provided small marshmallow pieces when the marmoset chose the arm that contained the rewarded stimulus.

2.3.2.5 Maze pretraining

Animals were familiarised with the maze environment over a period of weeks. To begin with, animals were allowed to roam freely within the maze, and collect marshmallow rewards scattered over the floor of the maze. When animals were familiar

with the layout of the maze, a similar process was used, however rewards were dispensed using the turntable system at the end of each arm (a hole in the floor of the arm revealed a turntable based food hopper that contained a reward).

Animals were then trained using small food rewards to visit the same 'start arm' of the maze upon presentation of a square wave cueing stimulus. When animals were proficiently navigating the maze in order to obtain rewards from the inbuilt turntable system, they were tested on a single visual discrimination pair. Of the two arms that were used to display object stimuli, the arm that contained the rewarded stimulus was randomly assigned. As the animals became more familiar with the procedure, the number of trials within a session was increased. When animals were achieving 90% accuracy on 50 trial single discrimination sessions they were transferred to the experimental task.

2.3.2.6 Screen Calibration

The computer screen positioned at the end of each arm were of exactly the same make and type and were chosen with consecutive serial numbers so that they were as similar as was feasibly possible. A rudimentary10 point characterisation of the monitors was taken, and a linearization process (similar to the serial recognition methods) was applied (using an extended power function). This allowed me to present stimuli with predefined luminance and chromaticity ranges. As stimuli could appear on one of several monitors, an averaging process was applied to the spectral data in order to achieve the colour calibration.

A similar process was used to relate cone excitation values to an output RGB level as in the serial recognition methods, however the cone absorption spectra were modelled using the peak absorption values proposed by (Travis et al., 1988). As male marmosets have a range of possible cone fundamentals, a search routine was applied in order to produce stimuli that had a minimal difference in the cone excitation value based upon models that utilised the different possible cone fundamentals.

2.4 NEUROPHYSIOLOGY METHODS

2.4.1 Introduction

In order to compare study at behavioural and physiological levels, it was of interest to examine the underlying neuronal mechanisms that could be implicated in the way that colour contributes to the visual process. I chose to record the response of isolated single cells in marmoset V1. Cells in this area have clearly defined visual properties and a range of studies have effectively managed to obtain quantitative measures of cell response to various manipulations in the stimulus characteristics.

A range of studies have shown that cells in V1 show similar tuning properties when animals are awake or anesthetised. Recording cell response from awake animals is technically and logistically difficult, however is preferential as it avoids many of the possible confounds relating to the physiological state of the animal. I chose to use an anesthetised setup to investigate cell response due to the inherent difficulties in recording from awake marmosets, however awake and behaving recordings remain a possible route for future research.

2.4.2 Preparation

Extra cellular single neuronal potentials were recorded in the striate cortex of 3 common marmosets (New World: Callithrix Jacchus). All licensed procedures were carried out in accordance and with the guidelines of the Animals (Scientific Proceudres) Act 1996. The methods that were employed have been previously detailed in (Webb et al., 2002).

Anaesthesia was induced using Saffan (Alphadalone/Alphaxalone acetate) (1.5mg/kg) and Ketamine (8mg/kg). These were administered intra muscularly (im). During the preparatory surgery depth of anaesthesia was monitored using the leg withdrawal reflex. Additional doses of Saffan were administered when required. Venous cannulation of the lateral tail vein was performed, allowing the continuous administration of fluids via an intra venous route (iv). The trachea was also cannulated to allow the animal to be artificially respired. In males the urethra was catheterized so fluids could be expelled from the bladder during the course of the experiment.

Once the preparatory surgery had been completed the animal was positioned within a sterotaxic frame. The head was mounted within the frame using ear bars coated with lidocaine hydrochloride gel. A bite bar was utilised as were eye hooks. An electric blanket (Harvard UK) was wrapped around the animal and body temperature was maintained near to 37 degrees using a rectal thermometer.

The animal was artificial ventilated. This was performed at a rate of 25-30 strokes per minute. Expiratory CO_2 levels were monitored using an HP Healthcare response centre (HP 78354C – HP UK). Respiratory pressure was adjusted to keep CO_2 levels between 30 and 40 mmHg. Anaesthesia was maintained using a gaseous mixture of 70% nitrous oxide (N_2O) and 30% oxygen (O_2). Fentanyl citrate was also administered (0.8ml/kg/hr iv). When the animal had been artificially ventilated skeletal muscles were blocked using Norcuron (vercuronium bromide) (0.05ml/kg/hr iv). Use of a neuromuscular blocker prevented eye movements during the course of the experiment. Cerebral oedema was prevented using colvasone (dexamethasone) (0.05ml/kg.hr iv). The fentanyl citrate, vercuronium bromide and dexamethasone were infused

intravenously in a volume made up to 1.5 ml/kg/h. The volume also contained a saline-glucose solution.

The head was fixed via means of a head post attached to the stereotaxic frame. The head post was mounted on the frontal bone using dental acrylic. Prior to head surgery isoflorane (fluothane) (0.05%) was included in the gaseous ventilation mixture. A craniotomy was then performed to allow access to the dura. A durotomy was then performed to expose the cortex within one hemisphere. The cortex was kept moist at all times using a saline solution.

The animals' EEG and ECG were recorded using Biopac hardware, this utilized acq32 software version 3.7 (BioPac Seattle). The ECG was filtered using a bandpass filter between 2 and 35Hz. This filtered signal was used to derive heart rate. The power spectrum of the ECG was also produced. This gave the magnitude of the delta, theta, alpha and beta parts of the ECG waveform. I used this to monitor the depth of anaesthesia. Supplementary isoflorane was administered during the experiment if required (between 0.05 and 0.1%). Ceporex (cefalexin) (Schering Plough Animal Health Ireland) was administered every 24 hours (0.25ml) to prevent bacterial infection.

2.4.3 Optics

Pupils were dilated using atropine sulphate (Antigen Pharmaceuticals Ireland), The animals eye lids were sutured and gas permeable contact lenses were used to protect the eyes. The lenses had zero added power, the position of the optic disks were plotted using a reversing ophthalmoscope.

Stimuli were presented using EXPOX version 2.0 or EXPOX version 1. The program was run using the same Macintosh computer that recorded waveforms. This was fitted with a NuVista and Radeon graphics card connected to a Sony Multiscan GDM200PDST monitor. Refresh rate was set at 120Hz. The monitor was calibrated to take into account various screen non-linearities. Receptive fields were plotted using a Electrohome marquee 8500 projector (Reflex UK). This projected to a large screen placed at a viewing distance of 57 cm. Once the receptive field had been found a mirror was used to redirect gaze towards the Sony monitor placed at a viewing distance of between 57 and 114 cm.

2.4.4 Recording

Recordings of single unit activity were performed using a tungsten microelectrode (FHC ME USA). The position of the microelectrode was altered using a significant digitimer microdrive (Digitimer Ltd UK). Signals were amplified using a HS4 digital bioamp headstage amplifier and DB4 controller module (World Precision Instruments FL USA). The amplified signal was monitored using an AM9 audio monitor (Grass RI USA) Waveforms were visualized using an HP 54603B oscilloscope (HP UK) and Hameg HM507 oscilloscope (Hameg).

2.4.5 Computer

The amplified signal was processed by a Macintosh G4 computer running Mac OS 9.1 or Mac OS X (Macintosh UK). The processor sorted action potential waveforms according to their shape and amplitude. Waveforms were recorded and time stamped with a resolution of 100 s. When the end of a penetration site was reached, the end of

penetrations were marked using lesion making apparatus. This dispensed a current of 5 a to the tip of the electrode for 10 seconds.

2.4.6 Cell classification

Receptive fields were characterised by varying the properties of drifting gratings displayed on the projector or the monitor. The process began with a large full field search grating being placed upon the projector screen. The achromatic grating had a drift rate of around 3Hz and spatial frequency of around 1 cycle/deg. Previous studies have shown that in macaque V1 the majority of chromatically responsive cells also respond to achromatic modulation (Lennie, Krauskopf and Sclar 1990). It was therefore not necessary to use a chromatically modulated search grating. The orientation of the search grating was continually varied so that cell response to gratings of all orientations was surveyed.

The electrode was gradually moved in 2 m steps until a reliable single cell response was observed. In some situations, the size, orientation, shape and spatial frequency of the grating was altered in order to isolate cells. Having determined estimates of the receptive field size of an isolated cell, a spike template was recorded.

At this point the stimulus presentation was redirected to the monitor. An assessment of whether the receptive field had a left eye dominance or right eye dominance was made, and corrective lenses were used to correct any refractory errors (refractory errors were assessed once per animal). Cells were classified as to whether they were simple or complex and the corresponding measure was used to assess cell

responsiveness (PSTH FT amplitude extracted at the optimal temporal frequency for simple cells and average spike count for complex cells).

Tests were carried out in order to determine the optimal size, shape, DKL vector, orientation, temporal frequency, spatial frequency and position of the grating that provided a maximal cell response. When these tests were concluded then the cell was assessed using the experimental programs detailed in chapters 7-8.

2.4.7 Screen Calibration

A 256 point characterisation luminance profile of the CRT gun phosphors was undertaken using a standard photometer upon any change in the experimental setup. The contrast and brightness of the monitor was adjusted to avoid saturating the signal amplifier. The data were collected using MATLAB, and then entered into a spreadsheet that calculated a gamma correction table. The linearized CLUT was used by the software to control luminance output. In one version of the stimulus presentation software that I used (EXPO) this stage was not necessary. An extended power function was used to characterise the luminance output and the parameters of this function were entered directly into the experimental software, The RMS error for each of the guns is provided in the appendices section 10.1.4.3.

2.4.8 Histology

At the end of the experiment the animal was given 0.1 ml of heparin to aid the perfusion and an overdose of Saffan. As soon as the ECG and EEG indicated that the vital signs had disappeared then the animal was perfused through the left ventrical of the heart. This was done initially with saline and then with 10 % formaldehyde (pH 7.4).

The brain was placed in a fixative solution containing 30 % sucrose. The brain was then sectioned using a freezing microtome (40-50 m). Sections were mounted and then stained using Thionin (Sigma UK). Tracts were reconstructed and cells assigned to anatomical areas and levels.

Figure 2-7 shows the histology for a medial to lateral section of the posterior part of one of the animals brains (MA42). As can be seen from the figures, the V1 / V2 is clearly defined by the red arrows. All penetrations were observed to be in V1. Although it was possible to differentiate between the layers (Figure 2-8) cells were not assigned to a specific layer due to the inherent difficulties in the process. Although we had information relating to the depth of each cell, individual differences between animals and disturbances of the cortical surface caused by the penetration track made assigning cells to a layer difficult.

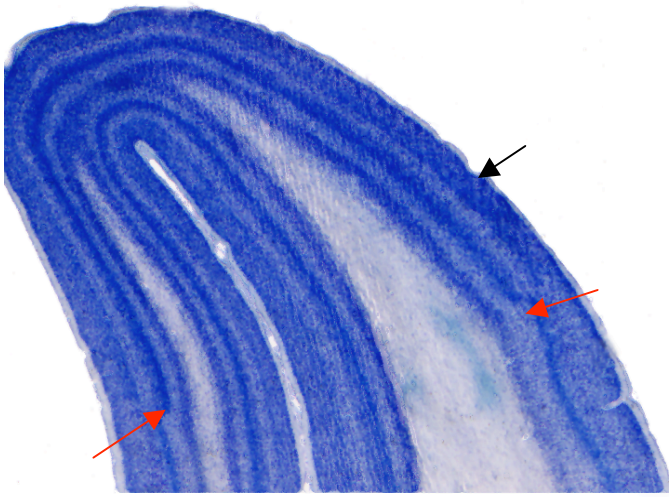

Figure 2-7: V1 Section, taken from medial to lateral sections of the left hemisphere of MA40. Red arrows indicate V1 V2 boundary. Black arrow shows location of penetration.

Figure 2-8: The same section as detailed in figure 6, rotated so that the cortex surface is horizontal. Dip in surface of cortex caused by electrode penetration.

Chapter 3 THE RELIABILITY OF THE SERIAL RECOGNITION PARADIGM AS A MEASURE OF HUMAN RECOGNITION MEMORY FOR OBJECTS CONTAINING CHROMATIC AND ACHROMATIC MODULATION

Experimental questions

Are the chromatic and achromatic visual sensitivity thresholds for simple object discrimination different?

Do subjects show response bias when tested using the serial recognition paradigm and normalised colour objects?

Does the combination of serial recognition task and threshold normalised stimulus provide steady state recognition memory?

3.1 INTRODUCTION

This chapter examines the product of combining data relating to the properties of the chromatic and achromatic visual detection mechanisms with a test of recognition memory. The ability of the resultant paradigm to produce an unbiased and constant measure of visual recognition memory is assessed within the context of other similar recognition memory techniques.

3.1.1 Discrimination thresholds for different visual detection mechanisms

Current models of visual processing describe the retinogeniculate visual pathway as comprising of two chromatic opponent mechanisms and one luminance opponent mechanism (see introduction). Characterising the properties of these opponent mechanisms is of importance in understanding the role that chromatic and achromatic sensory modulation has in visual perception.

Detection thresholds reflect differences in the way that the chromatic and achromatic mechanisms respond to stimuli. As these depend upon the spatial scale of the stimulus, the contrast sensitivity function has been adopted as a measure of mechanism sensitivity across multiple spatial frequencies.

Differences between the contrast sensitivity functions of the red-green, blue-yellow and luminance mechanisms have been found by a number of studies (Mullen, 1985, Cavonius and Estévez, 1975, Kelly, 1983, Hess and Pointer, 1989). Red-green detecting mechanisms are reported to be more sensitive to spatial or temporal luminance modulation than blue-yellow mechanisms (Cavanagh et al., 1987).

These findings are disputed by studies that report similar contrast sensitivity functions for red-green and blue-yellow mechanisms (Sekiguchi et al., 1993). By compensating for transient mechanism contributions to the red-green opponent pathway, normalised contrast response functions for the red-green and blue-yellow opponent systems have also been demonstrated to be similar (McKeefry et al., 2001). In order to control for the contribution of these mechanisms in tests of recognition memory, clarification is required of the relative visual sensitivity thresholds.

3.1.2 Tests of object recognition: controlling for differences in the visual sensitivity of the achromatic and chromatic visual detection mechanisms

Despite the potential differences in chromatic and achromatic thresholds, a number of tests of recognition ability have disregarded differences in stimulus achromatic and chromatic content. This is potentially troublesome if models of visual processing are to be extended to the domain of visual recognition memory.

Studies of recognition memory using a variety of techniques have shown that humans display an ability to retain information relating to coloured objects or scenes (Nickerson, 1965, Shepard, 1967, Standing, 1973, Homa and Viera, 1988, Suzuki and Takahashi, 1997). However differences in contrast sensitivity between the various visual detection mechanisms could introduce uncontrolled variance into experimental data collected using these techniques.

Where researchers have investigated the role of sensory factors (such as contrast), studies have found memory performance to be asymptotic when stimuli are visible (Wichmann et al., 2002). Despite this findings, questions remain concerning the

relative performance and reliability of data collected using stimuli that are unmatched in contrast. When these factors are accounted for, clear trends emerge relating to the differences between the contribution of the chromatic and achromatic mechanisms. This is shown in global shape discrimination tasks, where the observers threshold for discriminating form is measured (Mullen and Beaudot, 2002). In the study, the authors report that blue-yellow stimuli are discriminated less well than red-green stimuli and red-green stimuli are discriminated less well than achromatic stimuli.

3.1.3 Tests of object recognition: accounting for subject response bias

Another source of potential error in measures of recognition memory is that of subject response bias. Response bias arises when a subject over-classifies or under-classifies a series of stimuli as familiar. A number of studies have found little or no response bias for balanced 2IFC tasks (Green and Swets, 1966). However, for single stimulus designs, several studies have found response bias to be much larger (for a review see (Luce, 1997)). Researchers have therefore employed specific measures to account for these biases. There is debate over the necessity and suitability of the various correctional methods.

Signal detection theory (outlined in the general methods) relates to the process of making a decision in the presence of uncertainty. Calculation of a discriminability index (d') has been applied to data relating to neuronal response, psychophysical detection and recognition memory (Doty and Savakis, 1997, Newsome et al., 1989, Pelli, 1985, Green and Swets, 1966). One of the main assumptions of this framework is that the underlying distributions of signal and noise are normally distributed. As such an

assumption is rarely satisfied with empirical data, there is dispute of the appropriateness of this technique in calculating a measure of recognition ability (Aaronson and Watts, 1987).

For this reason alternative non-parametric methods have been proposed. The measure of A' relates to the probability of a correct response in a forced-choice procedure without response bias (Pastore and Scheirer, 1974). The advantages of A' are that it avoids assumptions about the signal and noise probability distribution functions (PDF). Despite this alternative framework, many researchers suggest that these assumptions are valid and the more commonly used measure of d' is appropriate.

It is of methodological importance to examine whether data collected using the methods outlined in this chapter requires corrections to be applied and to assess the suitability of any potential corrective measures.

3.1.4 Tests of object recognition: - does the serial recognition paradigm measure recognition memory under conditions that can be described as steady state?

Recognition tests often employ list-learning techniques to assess recognition ability over a specific time lag. These studies are prone to serial position effects, associated with stimulus primacy and recency. Researchers have attempted to overcome these biases using randomisation or counterbalancing techniques.

An alternative approach is to interleave study and test items, to produce a test of continuous serial recognition. The serial recognition (or continuous recognition) task allows stimuli to be presented and tested simultaneously using a number of delay lags,

thus overcoming serial position effects. It has been claimed that such tasks measure memory under conditions approaching steady state (the subjects displays a constant overall level of response over the time course of the experiment) (Shepard and Teghtsoonian, 1961). Such a situation is of benefit as it avoids potential bias that could be introduced into experimental data.

A number of studies have employed this paradigm to assess recognition memory (Kane et al., 2000, Doty and Savakis, 1997). However few measures are provided as to whether the task measures recognition performance under steady state conditions. The question therefore remains as to whether such a task provides memory that can be considered as steady state.

3.1.5 Developing tests of object recognition: - combining sensory achromatic and chromatic threshold measures with recognition measures

In this chapter a technique is outlined that addresses all of the above questions by using data relating to the visual detection mechanisms to normalise stimuli and then testing them in a continuous test of recognition memory.

Measurements were taken of the sensitivity of the chromatic and luminance visual detection mechanisms. Based on previous findings, it was expected that the red-green thresholds, the blue-yellow thresholds and the achromatic thresholds would be significantly different.

The obtained thresholds were used to create stimuli that were restricted in the range of their constituent chromatic and luminance variations. This had the effect of

normalising the response in each of the low level mechanisms. It was of both theoretical and practical interest to examine the effect that this had on general recognition performance for full colour stimuli (in terms or performance level, bias and practice effects).

Ideally the resultant recognition task would produce an overall level of recognition ability similar to the level of performance found in studies using naturalistic stimuli. It was predicted that the nature of the stimulus in terms of its flower-like resemblance (see general methods) and combination of luminance and chromaticity variations would produce such a level of recognition ability. It was also predicted that, due to the nature of the single-stimulus design used, subjects would show a degree of response bias, but that calculating a d' index would be an appropriate and sufficient means to overcome it. It was predicted that experimental data would meet the assumptions of normality required for this analysis.

It was of further interest to examine whether the combination of stimulus and task produced steady state recognition performance. Based on the non-verbaliseable nature of the stimuli used and the interleaved nature of study and test trials, it was predicted that recognition memory would be constant over the time course of the experiment.

3.2 METHODS

3.2.1 Design

Subjects performed two types of experimental task. The first task measured subjects' discrimination thresholds for the cardinal axes of DKL space (Diagram 1 in Figure 3-1). These were measured along the red, green, blue and yellow chromatic axes and the negative part of the luminance axis. Threshold values were used to normalise the colour space used in the two subsequent serial recognition tasks (Diagrams 2 and 3 in Figure 3-1).

Serial recognition sessions consisted of 406 trials (containing equal numbers of study and test trials). Flower type objects (detailed in general methods) were used as stimuli. Four groups of ten subjects were tested. Subjects indicated if objects appeared to be familiar or unfamiliar. On each trial a single object appeared centrally within the screen for a short period of time (2 seconds) followed by a blank inter-trial delay of 1 second.

On study trials subjects responded correctly when indicating that objects were unfamiliar. On test trials subjects responded correctly when indicating that objects were familiar. Study and test trials were interleaved so that the test object appeared after the study object with a delay of either one two or three intervening study or test objects.

Within each of the experimental groups, half of the objects were produced with ellipses coloured using negative luminance variations and an unrestricted chromatic spectrum (full colour objects). The other half of the objects contained various restrictions on their chromatic or luminance specifications (detailed in next chapter).

Only subject performance with full colour objects is considered in this chapter. Data were also averaged over all delay intervals in order to provide a general measure of recognition ability (differences between delay intervals are considered in the next chapter.

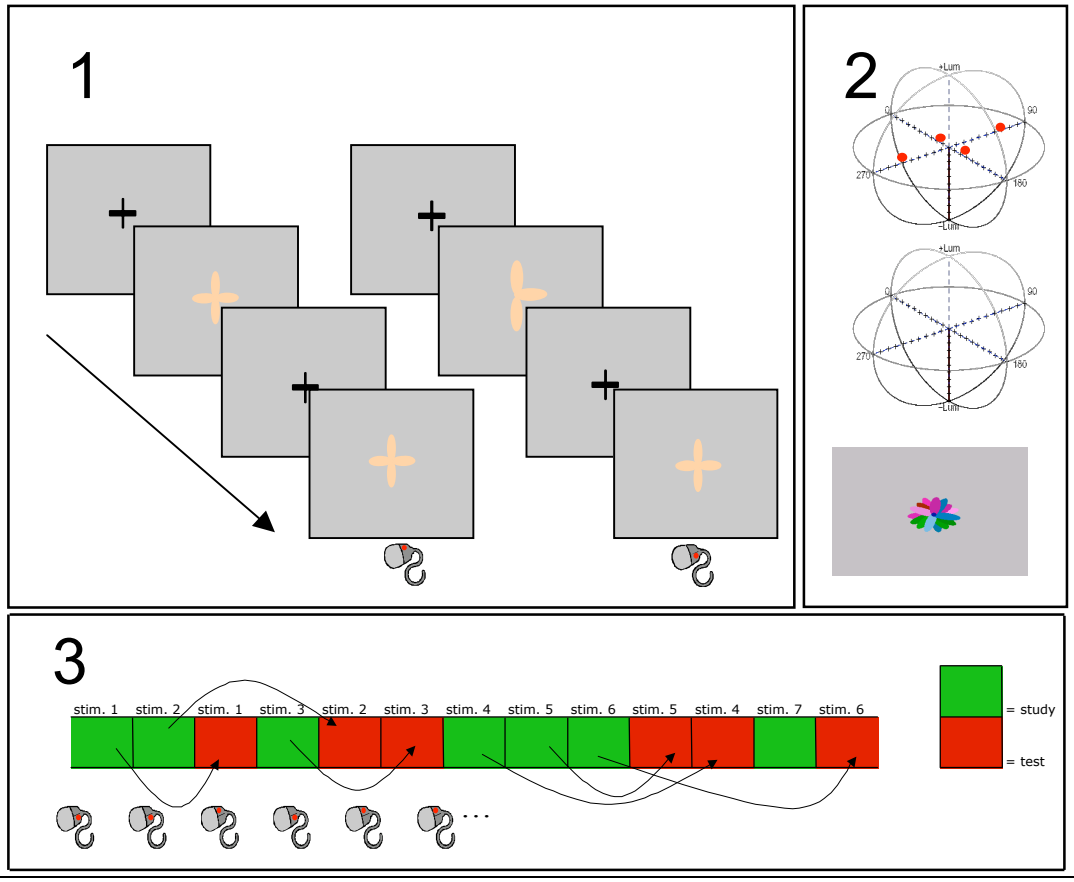

Figure 3-1: Experimental sessions: 1) Threshold sessions, determining discrimination thresholds for each of the cardinal axes of DLK space. 2) Threshold values (top sphere) used to normalise DKL space to a threshold based space (bottom sphere). Objects were then created using ellipses with DKL vectors that plot between two and four units along the cardinal axes of DKL space. 3) These objects were then used within the serial recognition task. Green boxes are study trials (novel objects) Red boxes are test trials (familiar objects).

3.2.2 Equipment

The task ran on a dual processor G4 Macintosh computer (Macintosh UK). Subjects provided responses via a two-button mouse (Kensington US). Feedback was provided using the computers' in-built speaker.

The experimental programs were programmed using MATLAB 5.2 (Mathworks UK), along with the additional PsychToolbox routines (Brainard, 1997). Experimental timing was derived from the system clock. Stimuli appeared on a Mitsubishi diamond pro monitor (Mitsubishi UK) driven by a Radius Golden Gate video card. Screen resolution was set at 640 by 480 pixels. A refresh rate of 60 Hz was used. Monitor output was linearized (see general methods).

Measurements of screen luminance and chromaticity were obtained using a PR-650 spectral radiometer (PhotoResearch US). Monitor output was described by an extended power function of the following form (shown for the green gun) (Brainard et al., 2001):

Equation 9: Function used to model the CRT luminance output.

$$g = [(G - G_0)/(1024 - G_0)]^{\gamma}$$

Where γ = the gamma exponent for the monitor, g = green-phosphor intensity, G = The DAC value for the green gun, G_0 = the cut off DAC value below which no light was emitted from the gun (For more details see general methods). This was chosen as it provided the best fit to the data obtained from measuring the phosphor output. The maximum achievable luminance output of the monitor was 83.273 cd/m^2. The maximum achievable output of each of the monitor phosphors are shown in .

Table 1. All objects appeared on a grey background of 41.6365 cd/m^2.

Table 1: The CIE xyY co-ordinates of the maximum output of the monitor phosphors.

	X	Y	Y
Red	0.6098	0.3463	18.2312
Green	0.2982	0.5997	55.4021
Blue	0.1499	0.0728	10.7736

3.2.3 Object structure

The objects tested in the experiment were produced using the flower type object algorithm detailed in the general methods.

Stimuli / Procedure

Threshold sessions used a self-paced, single stimulus, two choice procedure. Subjects were presented with a three-ellipse object (study object) for 2 seconds. Subsequently a short delay containing a uniform grey background and a centrally located fixation cross was presented. The fixation cross was removed and an identical three-ellipse object was presented (test object). This included a fourth element of variable contrast. Subjects reported whether the two objects were similar or dissimilar.

Subjects' responses made it possible to determine if they were aware of the variable contrast element within the test object. If the element was supra-threshold then subjects would report the objects as dissimilar, if the element was sub-threshold then they would report the objects as similar.

The three-element objects consisted of ellipses positioned at 0 90 180, or 270

Figure 3-2: Examples of the full colour objects used in the experiment.

degrees. The vacant position was chosen using pseudo random techniques. Test objects contained ellipses positioned at 0 90 180, and 270 degrees. Three out of the four ellipses were set to the same orientation and contrast of the preceding study object. The fourth element was placed in the position that was vacant in the study object. The contrast of the fourth element in the tested object was varied over the time course of the session.

When subjects reported that study and test objects were similar, the contrast of the manipulated ellipse was increased. This continued until subjects reported that the study and test objects were dissimilar on more than 15% of trials. The contrast of the modulated ellipse was then decreased.

When the direction of the contrast modulation was changed, the step size of the modulation was halved. When the contrast change reached the minimum level allowed by the device, the threshold was recorded and the axis upon which the threshold was

being determined was changed. Thresholds were consecutively determined for the red axis, followed by the green axis, blue axis, yellow axis and luminance axis. This was an unconventional method of measuring threshold values, however it provided a reasonable estimate (as seen by the small amount of standard error observed between subjects).

3.2.4 Colour Space

The DKL space was scaled to produce a space normalised in terms of subject threshold (see general methods). This was used to generate the objects used in the serial recognition task. Chromatic vectors were plotted between two and four threshold units on their respective DKL cardinal axes. Luminance vectors were plotted in the negative part of the space and were also between two and four threshold units.

3.2.5 Subjects

47 subjects participated in the visual threshold task. Subjects' data were discarded from the serial recognition sessions if average d' score in the first delay interval was below two, or if average d prime score for full colour objects was negative. For this reason, data from 40 subjects were used to provide the general measures of recognition memory. The threshold data has been reported for the seven subjects that were excluded from the serial recognition analysis.

3.3 RESULTS

3.3.1 Chromatic/ luminance thresholds for simple object discrimination

The first experimental session established the chromatic and luminance thresholds for simple (4 ellipse) object discrimination. These thresholds were defined by the amount of luminance or chromatic contrast required to discriminate an element within an object from another object that did not contain the variable contrast element. It was expected that red-green, blue-yellow and achromatic objects would require different levels of contrast in order to discriminate between objects. If different threshold values were found then it would further justify the use of visually controlled objects in tests of recognition memory.

By establishing thresholds for very simple object discrimination (which subjects performed effortlessly), subsequent sessions could be produced that contained objects comprising of supra threshold elements matched by their visual threshold values. These thresholds were unique to both stimulus type and subject.

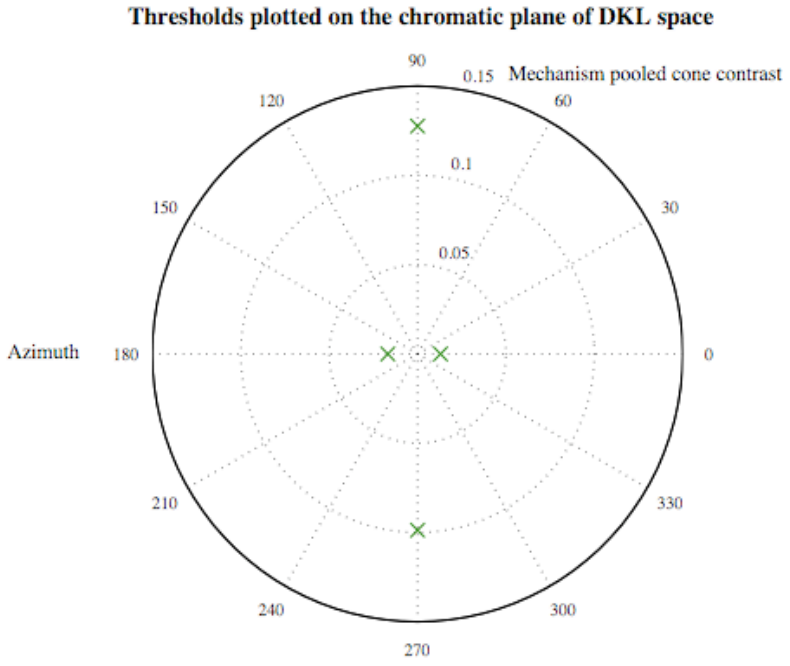

Figure 3-3: Visual discrimination thresholds plotted on the chromatic plane of DKL space. Units based on the mechanism pooled cone contrast.

Average threshold values were plotted on the chromatic plane of DKL space (Figure 3-3). The individual subject values were similar to the averages (as shown by the small standard error values detailed on the next page).

The centre of the diagram represents the device white point, the horizontal and vertical lines running through the midpoint relate to changes in the cardinal chromatic mechanisms.

DKL threshold values show an asymmetry between the two opponent chromatic mechanisms, the sensitivity of the blue-yellow system (vertical line between 90 and 270 degrees) being far less than the red-green system (horizontal line between 0 and 180 degrees.

Statistical analysis of group data for each of the threshold mechanisms (red, green, blue, yellow and luminance) produced a violation in the assumptions of normality (Mauchly's $W_9 = 0.008$ $p<0.001$). This could relate to the discrete nature of the data collected or the tendency of some subjects to provide an overestimate of threshold value. In either case, the violation can be accounted for in statistical procedures by applying an appropriate correction.

A greenhouse-geisser corrected ANOVA was run on the data from all groups to assess for significant differences in threshold level. A significant main effect of threshold colour was observed ($F_{1.463,65.848} = 223.91$, $p <0.001$, $\eta^2 = 0.833$, $\delta = 1$). Bonferonii corrected pairwise comparisons revealed significant differences at the < 0.001 level between all of the threshold types. The highest threshold value (or lowest contrast sensitivity) was produced for blue objects (DKL ΔR_S 0.1275 SEM = 0.0073) followed by yellow objects (DKL ΔR_S 0.0988 SEM = 0.0039), black objects (DKL ΔR_{LUM} 0.0503 SEM = 0.0026), green objects (DKL ΔR_{L-M} 0.0169 SEM = 0.00088) and red objects (DKL ΔR_{L-M} 0.0130 SEM = 0.00096).

Subjects therefore showed differential discrimination sensitivities for each of the cardinal directions of colour space. These differences could be due to the physiology of the eye, differences in the numbers of the various types of cone photoreceptor, morphology of the resultant mechanisms or weighting of resultant mechanisms. It was therefore important to take account of these differences when designing tests of recognition memory.

Having established the threshold values for each of the DKL mechanisms a version of the space was produced based upon these thresholds. Units within the space

were expressed by the multiple of visual threshold that experimental stimuli evoked within a mechanism. Using this space it was possible to create objects that were equated in visual threshold and contained elements that were all supra-threshold.

3.3.2 Overall measures of subject performance

Having equated stimuli in terms of visual threshold, a general measure of memory performance was taken for complex colour objects of the type shown in Figure 3-2. This was required in order to establish if the use of normalised colour objects reduced uncontrolled experimental variability (compared with other tests of recognition memory).

Overall memory performance was found to be adequate and reliable. Subjects provided a correct response to the colour objects on 78% of trials (SEM = 1.4%). This compares with a response accuracy of between 80% and 90% (SEM 5%) for a similar task using uncontrolled visual stimuli (Doty and Savakis, 1997).

The distribution of correct responses showed little skew (skewness = -0.065). Data showed a reasonable degree of kurtosis (kurtosis = -1.127). This suggested that the sample data approximated a leptokurtic distribution (subjects' scores near the mean were higher than would be predicted from a normal approximation). In spite of this the distribution of correct responses was not found to depart reliably from normality (Kolmogrov-Smirnov$_{40}$ = 0.126, p = 0.107).

Measures of subjects' performance were also taken using subjects' reaction times. Overall response time was found to be 1.06 s (SEM = 0.02). The distribution of reaction time data was normally distributed (Kolmogorov-Smirnov$_{40}$ = 0.122, p = 0.134,

skew = 0.376, kurtosis = -0.544). The combination of experimental task and trial unique colour stimuli produced data that provided an adequate and reliable level of recognition ability. The variability present within the data was less than observed in studies that failed to control for differences in visual sensitivity.

3.3.3 Bias in response

Biases in response could arise from subjects over or under-classifying objects as familiar or unfamiliar. This could have potentially produced misleading results. If subjects constantly responded to objects as familiar (an extreme bias) then they would correctly respond to half of the trials and all of the test trials. The subjects would not be discriminating between stimuli. If only the test trials were considered then they would achieve 100% accuracy. To assess the extent to which this happened, responses were categorised by the criteria shown in Table 2

Table 2: Definition of possible response types. Trial types are shown on the left hand side of the chart. Matrix of possible responses are shown on the right hand side of the chart

Trial Type	**Correct Response**	**Incorrect Response**
Study (new)	Correct Rejection	False alarm
Novel object	*(Identified as unfamiliar)*	*(Identified as familiar)*
Test (old)	Hit	Miss
Familiar object	*(Identified as familiar)*	*(Identified as unfamiliar)*

When data were averaged over the group, little difference was observed between correctly identifying a coloured object as being seen before (Hits = 77.74%) and correctly rejecting coloured objects as being unfamiliar (Correct rejections = 78.18%).

This difference was not found to be significant (t_{39} = -0.175, p = 0.862). Therefore, at the group level, no bias in subject response existed.

Further analysis examined the relationship between these scores at the single subject level. This was due to the fact that overall biases could be reduced by averaging over subjects.

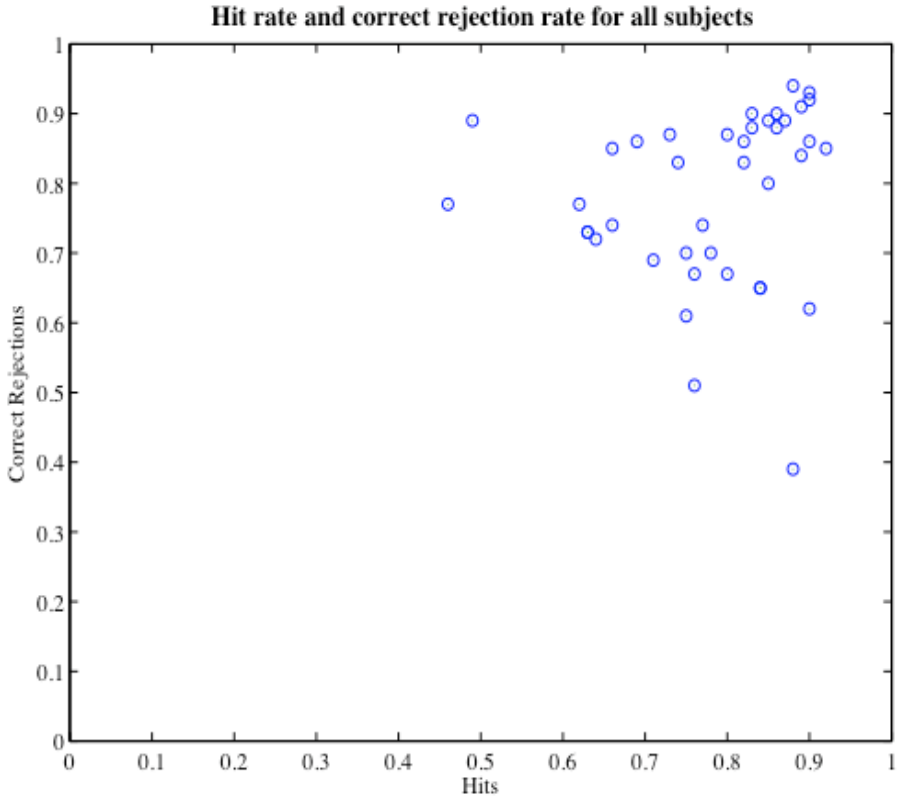

Figure 3-4: Average hit and correct rejection rate for all subjects.

Subjects' hit and correct rejection rates are shown in Figure 3-4. A number of subjects produced a differential ability in correctly identifying objects compared with correctly rejecting them. This is shown by the non-linear distribution of subject scores.

A Pearson product-moment correlation coefficient was calculated for the data shown in Figure 3-4 (subjects' hit and correct rejection rates). There was little or no relationship between subjects' hits and correct rejections ($r = 0.132$, $p = 0.418$). If there was no bias in subject scores, then a strong linear relationship would have been present.

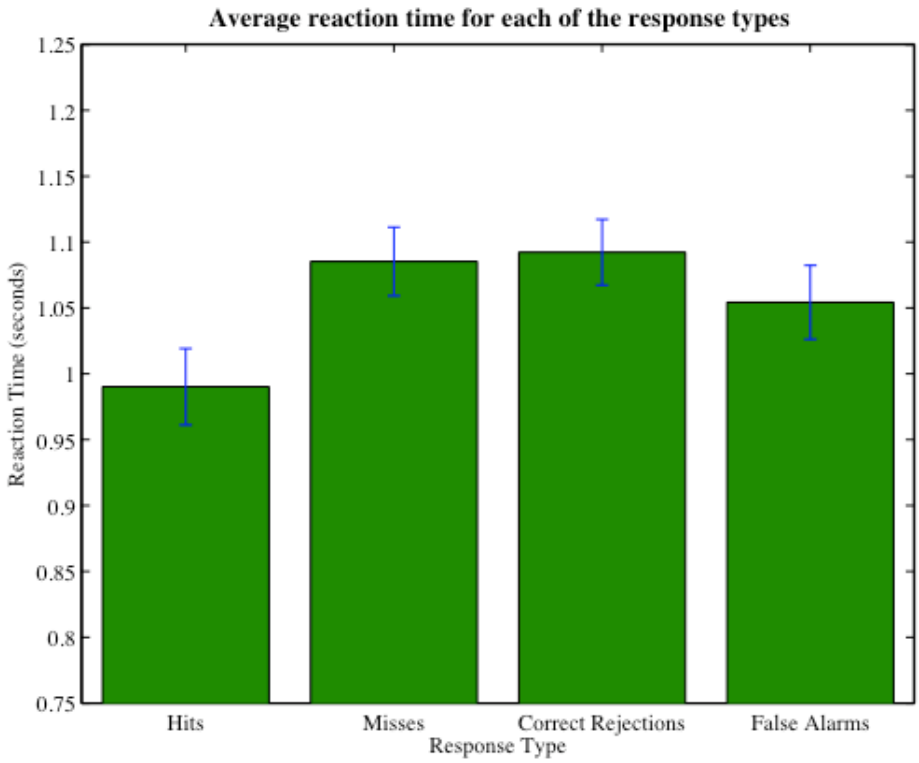

Figure 3-5: Mean reaction times for each of the different response types. Hit = correct response to a previously seen object. Miss = incorrect response to a previously seen object. Correct Rejection = correct response to a novel object. False Alarm = incorrect response to a novel object.

A further indication of potential response bias could be found in subject reaction time. Reaction time data for full colour objects was also classified by response type. Comparison of subject reaction times for each of the response types (see Figure 3-5), shows subjects provided differential reaction times. This was confirmed by a factorial repeated measures ANOVA (Data meets assumptions $W_5 = 0.771$, $p = 0.081$: $F_{3,117} =$

16.021 $p < 0.001$ $\eta^2 = 0.291$ $\delta = 1$). Pairwise comparisons (Bonferonii corrected) revealed that subjects provided a significantly faster response for hits (RT = 0.990) than for correct rejections (RT = 1.092) ($p < 0.001$), false alarms (RT = 1.054) ($p < 0.001$) and misses (RT = 1.085) ($p < 0.001$).

It was shown that with both subject response type and reaction time, ability to correctly recognise a coloured object was not a good predictor for the ability to correctly reject a coloured object as unfamiliar. When responses were averaged over all subjects then group data showed little bias in response; however, at the single subject level, biases could be observed. It was therefore decided to use a measure of discrimination ability that corrected for differences in these abilities. The different response types were combined to produce a discriminability index (d') or d prime score. This is a measure of the separation divided by the spread of the underlying distributions that represent the signal and noise inherent in a decision making process.

3.3.4 Steady state memory

Original studies of serial recognition claimed to measure recognition memory under conditions approaching steady state. As study and test stimuli were interleaved in a similar way, it was proposed that subjects' data contained no temporal biases in recognition memory.

It was of methodological and theoretical interest to measure whether the unique design and stimulus type used in this task produced a steady state of retention ability (as in previous studies). I therefore compared subject performance on full colour objects averaging across trials at various points during the time course of the experiment.

Subjects performed two identical sessions consisting of trial unique stimuli. Individual subject discrimination scores for colour objects in each of the experimental sessions are shown in Figure 3-6.

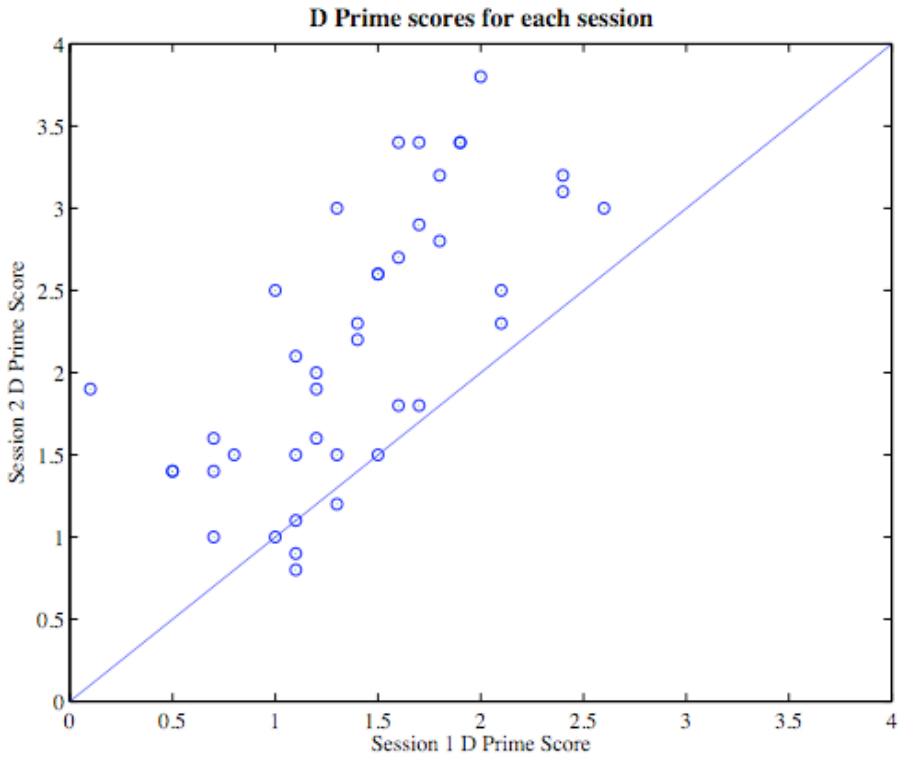

Figure 3-6: Individual subject discrimination scores for sessions one and two.

The majority of subjects show higher discrimination scores for the second session than the first session (points plot in upper left quadrant of chart). The data were reasonably strongly correlated (Pearson product moment correlation coefficient = 0.688, $p < 0.01$). This suggests that subjects' discrimination scores in the two sessions are related. Despite this finding subjects produced a significantly higher score in session 2 (d' = 2.195) than in session 1 (d' = 1.4175), $t_{39} = 8.090$ $p < 0.001$.

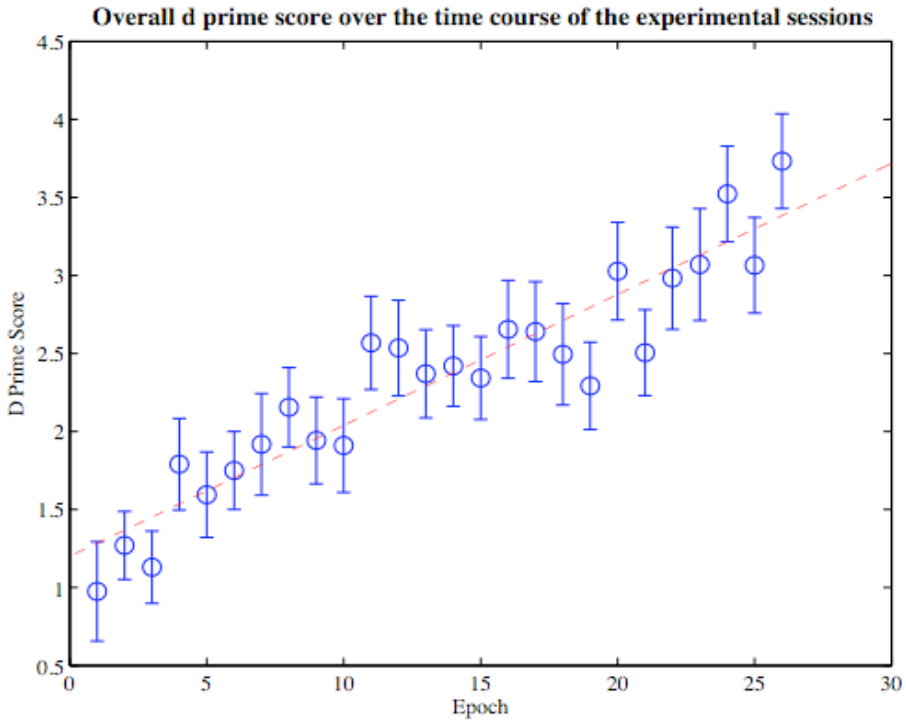

Figure 3-7: Overall subject discrimination ability across the time course of the experiment.

Subjects showed an increasing ability in discriminating colour objects (Figure 3-7). The data points for each epoch were based on subject response averaged over 58 consecutive trials. For the group data an average increase of a factor of 3.68 was observed between the first epoch and the last epoch. This showed that the subjects were learning within the time course of the experimental session.

In order to classify the nature of the increase in discrimination scores, a function was optimised to account for the trends in the data. Using linear regression techniques, the data was fitted using a linear function of the form

Equation 10

$$\hat{Y} = bX + a$$

Parameters were found to equal the following values:

$b = 0.08$

$A = 1.99$

($R = 0.933$, R^2 0.870, Adjusted $R^2 = 0.865$, t_A=11.725, $p = 0.001$, t_B= 12.680 $p = 0.000$).

The increase in discrimination ability was therefore found to be linear. As the distribution of different experimental manipulations (detailed in the next chapter) was evenly distributed across the time course of the experimental session, it was proposed that the increase in subject discrimination ability would not bias any of the experimental conditions (data were averaged over time).

3.4 DISCUSSION

3.4.1 Overview of experimental results

Subjects showed significantly different sensitivity thresholds for each of the DKL directions tested. Thresholds were used to generate colour objects containing controlled variations in luminance and chromaticity. Subjects showed an adequate ability to recognise these objects (78%, SEM 1.4%). Varying levels of bias were produced towards over classifying or under classifying objects as familiar. There was no pattern in the type or level of bias subjects produced (correlation between hits and correct rejections r = 0.132). Analysis also revealed a temporal bias in response, subjects getting better at the task as they progressed through the session. The significance of these results in developing a controlled test of recognition memory is discussed.

3.4.2 The role of visual sensitivity thresholds in normalising the visual properties of object stimuli

Measuring the properties of the chromatic and achromatic mechanisms was necessary in order to develop a test of recognition memory where differences in visual sensitivity were controlled. Our results showed the highest contrast sensitivity values for the red-green mechanism, followed by the luminance mechanism and the blue-yellow mechanism. These findings are convergent with studies using sinusoidal gratings. Tests of foveal contrast sensitivity at all but low spatial frequencies (< 0.4 cyc/deg) produce similar results (Mullen and Kingdom, 2002).

Where studies have failed to find differences in contrast sensitivity between mechanisms, possible theoretical and methodological reasons could explain the

discrepancy. In one study, stimuli were presented at high luminance levels that favoured less sensitive mechanisms (Sekiguchi, Williams et al. 1993). In another study, contributions of transient mechanisms were accounted for by normalising the red-green sensitivity by a factor of 1.5 (Sekiguchi et al., 1993, McKeefry et al., 2001). The extent and role that these transient mechanisms play in chromatic detection are currently debated and so conclusions based upon possible interactions have to be interpreted with caution.

Higher red-green and achromatic contrast sensitivity values could be related to the predominance of L and M cones in the retina compared to S cones (Curcio et al., 1990, Mollon and Bowmaker, 1992). There is also a physiological distinction between red-green and blue-yellow post-receptorial mechanisms. It has been proposed that blue-yellow modulation is conveyed through midget bipolar and small bistratified cells (Dacey and Lee 1994, Dacey, 1993a, Mariani, 1984). Signals from these classes of cell are then relayed along the koniocellular layers of the LGN (Martin et al., 1997). Separate retinal circuitry conveys red-green modulation. Signals originate in the parvocellular midget cells and are relayed through the corresponding layers of the LGN. Studies have found a degree of overrepresentation of the visual field in LGN parvocellular layers. This could also account for increased red-green and achromatic sensitivity (Azzopardi et al., 1999).

3.4.3 The reliability of the paradigm in obtaining a measure of recognition memory for full colour objects – response bias

Measures of response bias (the ratio of hits to correct rejections) displayed no apparent relationship between the hits and correct rejections ($r = 0.132$). This suggested

that subjects were biased towards either over-classifying or under-classifying stimuli as familiar. Such biases have been shown in a number of single-stimulus designs and can be eliminated by varying the probability of presenting test stimuli or reward for correct responses (Hautus and Collins, 2003). In this study, subject bias was evenly distributed between the tendency to overestimate or underestimate stimulus familiarity. For this reason, such a procedure could only work at a single-subject level. It was decided not to apply such a correction as it would introduce a potential confound to between subject comparisons. To overcome the observed response bias, a d prime (d') index was calculated.

A degree of criticism has arisen over the reliability of d' as a test of perceptual discrimination. This is based upon the fact that payoff and probability manipulations do not effect decision criteria (Balakrishnan, 1998a, Balakrishnan, 1999). However these arguments have been subsequently shown to be flawed (Treisman, 2002). A further assumptions of the d prime correction is that distributions of the signal and noise used to form the subjects' decision can be modelled by a normal probability distribution function. It would be practically challenging to obtain such measures for the task employed, however in the context of the current study the distributions were assumed to be normal. Evidence for this assumption is based on previous literature (Green and Swets, 1966).

3.4.4 The concept of steady state memory in the serial recognition paradigm

Sources of temporal bias were also observed in subject response. These could not be corrected using the above framework. Subjects tended to provide higher levels of

recognition ability over the time course of the experiment (a factor of 3.68 over 40 minutes). Recent studies that utilise a similar paradigm fail to provide a measure of overall ability across the time course of the experiment (Doty and Savakis, 1997, Kane et al., 2000).

Where studies have shown increases in recognition or discrimination ability over the extended time periods, the periods in questions tend to be significantly longer than those employed in this study (day, weeks or months). These include the perceptual learning studies that propose visual mechanisms as responsible for increases in ability (Ghose et al., 2001, Matthews et al., 2001, Sowden et al., 2002). The time course of perceptual learning (day or months) therefore could not account for the increases in discrimination ability found within this study.

Seminal work reported the serial recognition paradigm as providing conditions for the retention of information that approached steady state (Shepard and Teghtsoonian, 1961). This contradicts the findings of increases in recognition ability. In this task, the maximum lag between study and test (up to 4 trials or 10 seconds) was much shorter than in the original studies of recognition memory. This difference could allow subjects to develop a strategy for recognising objects. When questioned about their recollection of the nature of the task, subjects were unaware of the configuration of the study and test trials.

Other possible reasons for the discrepancy relate to the stimulus type used in the task. Trial-unique non-verbalisable visual stimuli have a history of providing a reliable test of recognition memory. A naturalistic version of this type of stimulus was used. Despite this, it is possible that subjects could have developed strategies for remembering

objects by attaching a verbal tag to certain elements within an object. The arguments against this scenario are twofold. Firstly, subjects were not given enough time to easily verbalise stimuli. Secondly, overall there was not a significant bias between correct rejections (where no strategy could have been used) and hits.

3.4.5 Conclusion

In conclusion, the test of recognition memory I produced provided an adequate level of memory performance, similar to that found with tests of photorealistic equivalent objects. The test controlled for the differing sensitivities of the chromatic and achromatic mechanisms. This was achieved by normalising the visual properties of stimuli in DKL space.

The test also controlled for the subjects over or under classifying objects as familiar by reporting subjects' ability using d prime scores. This corrected for the response biases observed at a single subject level. The test did not produce recognition memory performance that could be described as steady state. This could be due to subjects developing strategies to label object stimuli. To overcome this increase in recognition ability, data averaged over two equivalent sessions were used with equal numbers of trial types. This technique is used in the following chapter.

Chapter 4 MEASURES OF HUMAN OBJECT RECOGNITION FOR STIMULI LACKING; CHROMATIC, LUMINANCE, RED-GREEN, AND BLUE-YELLOW VISUAL MODULATION

Experimental questions

Does the selective removal of luminance modulation or chromatic modulation from an object affect the ability to discriminate that object from similar objects?

Does the selective removal of the chromatic signals carried by one or more of the two opponent pathways (red-green & blue-yellow) have differing effects?

Do chromatic signals play an equivalent role in object discrimination at different delay intervals?

4.1 INTRODUCTION

Colour conveys an advantage in tasks of recognition memory. Removal of stimulus colour has been shown to degrade performance in recognising various types of natural stimuli. These include natural scenes (Wichmann et al., 2002, Oliva and Schyns, 2000, Gegenfurtner and Reiger, 2000), faces (Lee and Perrett, 1997), degraded faces (Yip and Sinha, 2002) and food objects (Wurm et al., 1993).

What is the nature of the advantage that colour provides? Some authors emphasis the role of colour in low level visual segmentation (Mollon, 1989, Wurm et al., 1993). Others describe effects relating to the cues colour provides in the retrieval of previously encountered visual information (Humphrey et al., 1994).

In studies of visual recognition using scenes (Gegenfurtner and Reiger, 2000), research suggests that colour contributes to recognition in both of the above ways. For stimuli shown for very brief periods (16msec), recognition of images presented in colour was better irrespective of the type (colour or greyscale) of test image employed. This was interpreted as colour providing a coding advantage. At longer presentation times an advantage was observed for images presented and tested in colour, compared with images presented in colour and tested in black and white. When images were presented in black and white and tested in colour, no such facilitation was observed. The authors suggested that this advantage was produced due to a richer representation of the image in short-term memory (short term memory was implicated due to the nature of the asking technique used in the experiment).

Attempts have been made to relate effects of stimulus colour manipulation to underlying physiological mechanisms. Chromatic modulation is encoded using two opponent mechanisms that originate in the retina (red-green and blue-yellow). These systems have a number of distinct properties that have allowed researchers to speculate on various functional characteristics (for a review see introduction or (Dacey, 2000)).

Mechanism-specific deficits in object recognition have been produced using stimuli that isolate one or other of these systems. The blue-yellow mechanism has been shown to be impaired in processing object stimuli compared with the red-green system. Effects have been shown quantitatively in shape discrimination tasks (Mullen and Beaudot, 2002), and qualitatively in object recognition tasks (Stewart and Cole, 1989).

Evolutionary arguments have also been proposed that account for the functional advantage that red-green opponent mechanism provides. It has been suggested that this more recently evolved pathway was specialised for the purpose of detecting fruit from foliage (Mollon, 1989, Osorio and Vorobyev, 1996, Sumner and Mollon, 2000, Regan et al., 1998) or ripe leaves (Lucas et al., 1998).

If evolutionary arguments are consistent with experimental data then a difference in object recognition ability would be expected between dichromats (protanopes and deutranopes) who utilise a single blue-yellow opponent pathway in chromatic processing and trichromats (who utilise separate red-green and blue-yellow opponent pathways). Comparison of trichromat and colour blind dichromat human subjects shows no such deficits relating to the lack of the red-green pathway (Gegenfurtner et al., 1998). However the type of stimulus used in the study (natural scenes) may be of relevance.

The type of X-chromosome linked dichromats that were used have been shown to become partially trichromatic for larger fields (>2 degrees). Although the mechanisms that underlie this phenomenon are poorly understood, for the scene stimuli such as the type used by Gegenfurtner and colleagues, such an effect could influence recognition behaviour. Despite accounts of this nature, the subjects in the experiment would still have had problems discriminating between red and green, it is this deficit that is highlighted by the personal accounts of the observers. Dichromats generally report that they develop strategies to allow them to perform normally within the visual world, and only under specific circumstances (such as the detecting red fruit from a green foliage under a variable illuminate) do they have problems. Further studies could examine these circumstances.

In this study the effect of restricting various types of visual modulation was measured using an object discrimination task. Stimuli were created that lacked any variations in colour, luminance, red-green colour and blue-yellow colour. In order to assess the nature of effects caused by the restriction of various visual modulations, a modified version of the serial recognition task was used (Shepard and Teghtsoonian, 1961). This allowed the measurement of subjects' discrimination after several delay intervals. Measurements of visual discrimination thresholds of each of the cardinal directions of colour space (red, green, blue, yellow and black) were also taken. This was in order to equate the subjective intensity of different colours, reported by participants.

Based on previous studies of object recognition it was predicted that the removal of stimulus colour would cause a deficit in subject discrimination performance. It was also expected that this deficit would be apparent for restrictions in red-green colour but

not for blue-yellow colour. Due to the type of stimulus used and the nature of the paradigm, it was expected that these effects would be apparent at short delay intervals (when the task was sensory in nature) and not longer (memory based) delay intervals.

Removal of either all chromatic stimulus modulation or red-green stimulus modulation caused impairments in object recognition. Removal of blue-yellow colour or luminance modulation caused no impairment. Impairments were found to be greatest at short delay intervals between study and test objects.

4.2 METHODS

4.2.1 Design

The aim of the experiment was to measure the ability to discriminate trial-unique flower-like objects of different colours over different time periods. Each subject performed three sessions consecutively. These lasted for approximately one hour in total. In the first session, visual discrimination thresholds were obtained. These data were used to compensate for differences in contrast thresholds for the various colours employed to shade the objects (details in previous chapter). All of the visual elements contained within the objects were above threshold.

The two further sessions consisted of continuous serial recognition tasks (details in general methods). Each session contained 406 trials and lasted for 20 minutes. These sessions were intended to measure subject ability to discriminate the trial unique flower-like objects. The effect of two variables on discrimination ability were examined:

1) The effect of increasing the delay interval between study and test object.

2) The effect of restricting various types of visual modulation used to display the object.

All stimuli (study and test objects) remained on screen for 2 seconds, with an intervening uniform grey background replacing the object for 1 second. Test objects were presented after the study objects using one of four delay intervals. Test objects reappeared either immediately after the study object, or after 1, 2 or 3 intervening objects. The delay interval between study and test items therefore lasted for 1, 4, 7 or 10 seconds. Sessions contained equal numbers of study and test items. Equal numbers of

study and test items were also assigned to each of the delay intervals. Equal numbers of colour object and visually restricted objects were tested at each of the delay intervals (see Figure 4-1). Stimuli were restricted in their visual properties so they lacked:

Colour – Greyscale stimuli that only contained variations in luminance.

Luminance – Isoluminant stimuli that only contained variations in chromaticity.

Red-green colour – Stimuli that contained variations in luminance and blue-yellow colour

Blue-yellow colour - Stimuli that contained variations in luminance and red-green colour

Each group of subjects were tested on a set of objects, of which half of the objects contained variations in colour and luminance (full colour stimuli) and the other half contained one of the four visual restrictions. The aim of this design was to allow the within group comparison of full colour objects and objects lacking some form of visual modulation.

4.2.2 Equipment

The experimental equipment outlined in the previous chapter was used.

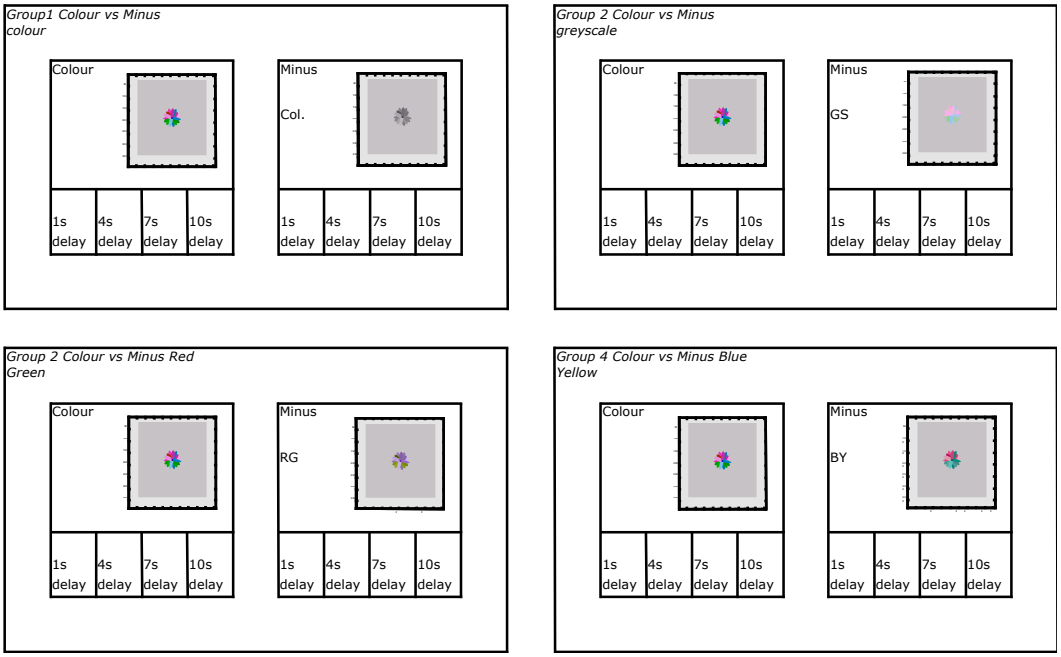

Figure 4-1: Representation of the experimental design: Each of the groups is based upon an independent sample of 10 subjects. Groups compare full colour stimuli with stimuli lacking colour, luminance, red-green colour or blue-yellow colour. Each stimulus type is tested at four delay intervals: Interval 1 = 1s delay between study and test. Interval 2 = 4s delay, Interval 3 = 7s delay, Interval 4 = 10s delay.

4.2.3 Stimuli

The objects tested in the experiment were produced using the flower type object algorithm detailed in the general methods. The parameters outlined in the previous chapter were used to construct the objects. The resultant objects are shown in Figure 4-1. The objects were constructed from ellipses whose colours were defined in DKL co-ordinates. All colours differed from background between 2 and 4 times thresholds (except for equiluminant stimuli). All variations in luminance were negative (along the

DKL luminance axis). All vectors plotted between two and four threshold units along the DKL axes.

Using the threshold based colour space it was possible to restrict the chromatic and luminance variations present within the objects. Four restrictions were applied:

1) Allowing no variations in chromaticity along the DKL chromaticity plane (minus colour objects).
2) Allowing no variations in luminance along the DKL luminance axis (minus luminance objects).
3) Allowing no variations in chromaticity along the DKL red-green axis (minus red-green objects).
4) Allowing no variations in chromaticity along the DKL blue-yellow axis (minus blue-yellow objects).

4.2.4 Subjects

The same group of subjects was used as reported in the previous chapter.

4.3 RESULTS

4.3.1 Effects of colour or luminance subtraction

4.3.1.1 *Measures of discrimination ability relating to the removal of stimulus colour*

In one group of ten subjects, I examined the effect of removing all chromatic variations present within an object by comparing discrimination performance with colour objects and greyscale objects. Data from this group was averaged over subject, session and delay type.

Data was found to meet the assumptions of normality using a Shapiro Wilks test. (Coloured stimuli: $D_{10} = 0.232$, $p > 0.05$; Greyscale stimuli $D_{10} = 0.184$, $p > 0.05$). The test is more reliable for groups of less than 50 than the more commonly used Kolmogorov-Smirnov test. The Kolmorgorov-Smirnov test was used in the previous chapter due to the fact that all (approaching 50) subjects provided valid threshold data thus making the group size more appropriate for this type of test.

A two by four repeated measures factorial ANOVA was used to assess significant differences between group means. ANOVA provides a good test of statistical difference as it accounts for multiple comparisons. This gives a greater amount of statistical power than using multiple t-tests.

A significant main effect of the visual properties of the stimulus (chromatic and luminance vs. luminance) was found ($F_{1,9} = 9.148$ $p < 0.05$, $\eta^2 = 0.504$, $\delta = 0.768$). Subjects produced significantly higher scores with coloured stimuli (d' = 2.08, SEM =

0.260) than with greyscale stimuli (d' = 1.655, SEM 0.336). Thus subjects performed better with the full colour objects than the objects lacking colour.

The observed power (δ) was computed using an alpha level of 0.05. The effect power details the ability to detect an effect should one be present. The η^2 value relates to the effect size obtained from the general linear model. It gives the amount of variability in the dependent variable that can be accounted for by the independent variable.

4.3.1.2 Measures of reaction time for chromatic and achromatic stimuli

The drop in subject performance due to the removal of object colour was also examined for subject reaction times. Reaction time data was taken for subject responses classified as 'Hits' or 'Correct Rejections'. Data was averaged over subjects, sessions and delay interval. Subjects did not appear to provide different reaction times for the various stimulus types (Col RT = 1.05 SEM = 0.046, GS RT = 0.969 SEM = 0.051).

Data was found to meet the assumptions required for ANOVA (Shapiro-Wilk: Colour $W_{10} = 0.927$, $p > 0.05$: Greyscale $W_{10} = 0.868$, $p > 0.05$). No significant main effect of stimulus colour was found for the reaction time data ($F_{1,9} = 1.584$, p. = 0.240, $\delta = 0.204$). There was therefore no difference in the time that subjects took to respond to colour versus greyscale objects.

4.3.1.3 Measures of discrimination ability relating to the removal of stimulus luminance modulation.

A second group of ten subjects were tested using full colour objects and equiluminant objects. The group examined whether a similar effect to that found with the removal of chromatic modulation was present when luminance modulation was removed.

Data was averaged over subject, session and delay interval to provide the mean d prime scores, for each of the stimulus manipulations. Subjects within this group provided similar d prime scores, for both stimulus types. Tests of normality using the Shapiro-Wilks test found the data to be normally distributed (Colour: $W_{10} = 0.860$, $p > 0.05$; Isoluminant $W_{10} = 0.877$ $p > 0.05$). There was no main effect of the colour manipulation ($F_{1,9} = 1.583$, p. = 0.240, $\delta = 0.203$). Removal of luminance modulation therefore had no effect on subject discrimination ability (Colour d' = 1.800 SEM 0.217, Equiluminant d' = 1.698 SEM = 0.1698).

In summary, subjects showed a significant deficit in their discrimination ability, caused by the removal of stimulus colour. This deficit was not observed when luminance modulation was restricted. This effect was also not present within the reaction time data.

4.3.2 Effects of selectively removing stimulus colour relating to the opponent pathways.

4.3.2.1 Measures of subject discrimination ability relating to the removal of colour conveyed by one of the chromatically opponent pathways

Two further groups of ten subjects were tested. This was in order to examine if the deficit in discrimination ability caused by the removal of stimulus colour was specific to one of the chromatically responsive opponent pathways (red-green or blue-yellow). Both groups studied two types of objects, full colour objects and objects that were restricted in their chromatic properties. For one group the restricted stimuli contained no red-green colour. For the other group, the restricted stimuli contained no blue-yellow colour. Results demonstrated that removal of red-green colour impaired discrimination ability but removal of blue-yellow colour did not impair discrimination ability.

Data in the group comparing full colour objects and objects lacking red-green colour was normally distributed: (Colour objects: $W_{10} = 0.950$ $p > 0.05$, objects lacking red-green colour: $W_{10} = 0.948$ $p > 0.05$). Normality was also found for the group comparing colour objects and objects lacking blue-yellow colour (Colour objects: $W_{10} = 0.954$ $p > 0.05$, objects lacking blue-yellow colour $W_{10} = 0.847$ $p > 0.05$).

Separate repeated measures factorial ANOVA's were performed on each of the two groups. A significant main effect was found for the group that contained stimuli lacking their red-green colour ($F_{1,9} = 5.119$, $p < 0.05$, $\eta^2 = 0.363$, $\delta = 0.524$). Subjects

performed significantly better with full colour stimuli (d' = 1.783, SEM = 0.160) than with stimuli lacking their red-green colour (d' = 1.568, SEM = 0.159).

A main effect of stimulus colour removal was not found for the group comparing full colour stimuli (d' = 2.075, SEM = 0.242) with stimuli lacking their blue-yellow colour (d' = 2.180, SEM = 0.208) ($F_{1,9} = 0.528$, p. = 0.486 $\eta^2 = 0.055$, $\delta = 0.10$). The main effect of colour subtraction for red-green objects but not blue-yellow objects shows a differential effect of colour subtraction based upon specific chromaticity.

4.3.2.2 Measures of reaction time across colour condition

Reaction time data was also examined. This was in order to assess whether the differential effect of red-green colour subtraction was also present in subject response times. No significant differences were found in the mean reaction times for stimulus type in both groups of subjects (Colour vs. minus RG: $F_{1,9} = 0.113$, p. = 0.744, $\delta = 0.061$, Colour vs. minus BY: $F_{1,9} = 0.253$, p. = 0.627, $\delta = 0.074$). Subjects provided similar response times irrespective of the chromatic properties of the stimulus:

Colour vs minus RG (COL RT = 1.109, SEM = 0.055, minus red-green RT = 1.096, SEM = 0.077)

Colour vs minus BY (COL RT = 0.983, SEM = 0.093, minus blue-yellow RT = 0.960, SEM = 0.066)

There was therefore no speed accuracy trade off (there was a difference in accuracy that was not accompanied by a change in reaction time).

4.3.3 Effects of increasing delay interval

4.3.3.1 Measures of discrimination ability across delay interval

For each of the four experimental groups, test objects were presented after one of four delay intervals. To assess the effect that increasing delay interval had on subject ability to discriminate objects, data were analysed over the various delay intervals.

In summary, effects of stimulus manipulation were largest at the first delay interval and were specific to the same classes of stimuli as shown by the main effects. Analysis was carried out separately for each of the various chromatic / luminance stimulus manipulations, in order to evaluate the effect delay interval had on subjects ability to discriminate the various stimulus classes.

All subjects were tested with equal numbers of each stimulus type within each of four delay intervals. Study objects were tested either immediately or after one two or three intervening trials. These intervals corresponded to a delay between study and test of one, four, seven or ten seconds. Data was averaged over all groups and subjects to produce mean discrimination scores for each of the four delay intervals.

Subjects displayed a decreasing ability to discriminate over the four progressive delay intervals (delay1 = 1s delay, delay2 = 4s delay, delay3 = 7s, delay4 = 10s) : (delay1 d' = 2.855, SEM = 0.134; delay2 d' = 1.754, SEM = 0.120; delay3 d' = 1.537, SEM = 0.123; delay4 d' = 1.274, SEM = 0.089) Separate factorial ANOVAs were used in the data analysis. This was due to the fact that one of the groups provided data that violated the assumptions of ANOVA (thus requiring compensatory measures). The group comparing full colour objects and objects lacking luminance modulation

(equiluminant stimuli) was found to violate the assumptions of ANOVA (W_5 = 15.717 p. = 0.008, epsilon = 0.460). A greenhouse-Geisser correction to the number of degrees of freedom was therefore applied to the results from this group.

Groups found to be normally distributed included the groups consisting of full colour objects vs.: Objects lacking colour (W_5 = 0.262 p. = 0.068), Objects lacking red-green colour (W_5 = 0.280, p. = 0.082), Objects lacking blue-yellow colour (W_5 = 0.2672, p. = 0.076)

Subjects showed a monotonic decrease in d' score as the delay interval increased, irrespective of stimulus colour. This effect was significant as shown by separate ANOVA's on each of the experimental groups:

Group	DF	F	P	Effect Size	Power
Colour v Minus Colour	13,27	26.4	<0.001	0.746	1
Colour v Minus Luminance	1.379,12.410	75.4	<0.001	0.893	1
Colour v Minus Red-green	3,27	49.4	<0.001	0.846	1
Colour v Minus Blue-yellow	3,27	58.9	<0.001	0.868	1

For all of the above groups pairwise comparisons revealed a significantly higher discrimination score in the first delay interval than in the second, third and fourth delay intervals.

In all groups other than the group comparing colour objects and objects lacking colour, subjects performed significantly better in the second delay interval than in the fourth delay interval. In the group comparing colour objects and objects lacking luminance modulation, subjects performed significantly better in the second delay interval than in the third delay interval.

A significant interaction was found between the stimulus manipulation and the delay interval manipulation for the group comparing full colour stimuli and stimuli lacking colour ($F_{3,27} = 2.923$, $p < 0.05$, $\eta^2 = 0.304$, $\delta = 0.769$). As the delay increase lengthened the difference between the mean values for discriminating the different stimulus types decreased.

A significant interaction between the stimulus type and delay interval was also found in the full colour vs. stimuli lacking red-green colour group ($F_{3,27} = 4.225$, $p < 0.05$, $\eta^2 = 0.319$, $\delta = 0.802$). As the delay interval lengthened the difference between the mean values for discriminating the different stimulus types decreased.

4.3.3.2 Fitting power functions

Curves were fitted to the data for each group in order to characterise the nature of the monotonically decreasing scores for the different classes of stimuli (Figure 4-2). The MATLAB fminsearch function was used to optimise the parameters of a power function of the form:

Equation 11

$$y = ax^{-b}$$

Optimisation was achieved using a Nelder-Mead simplex (direct search) method. The proportion of unexplained variance was minimised so that the function provided as close a fit to the experimental data points as possible. Table 3 gives the fraction of accounted for variance and fit parameters for each of the curve fits.

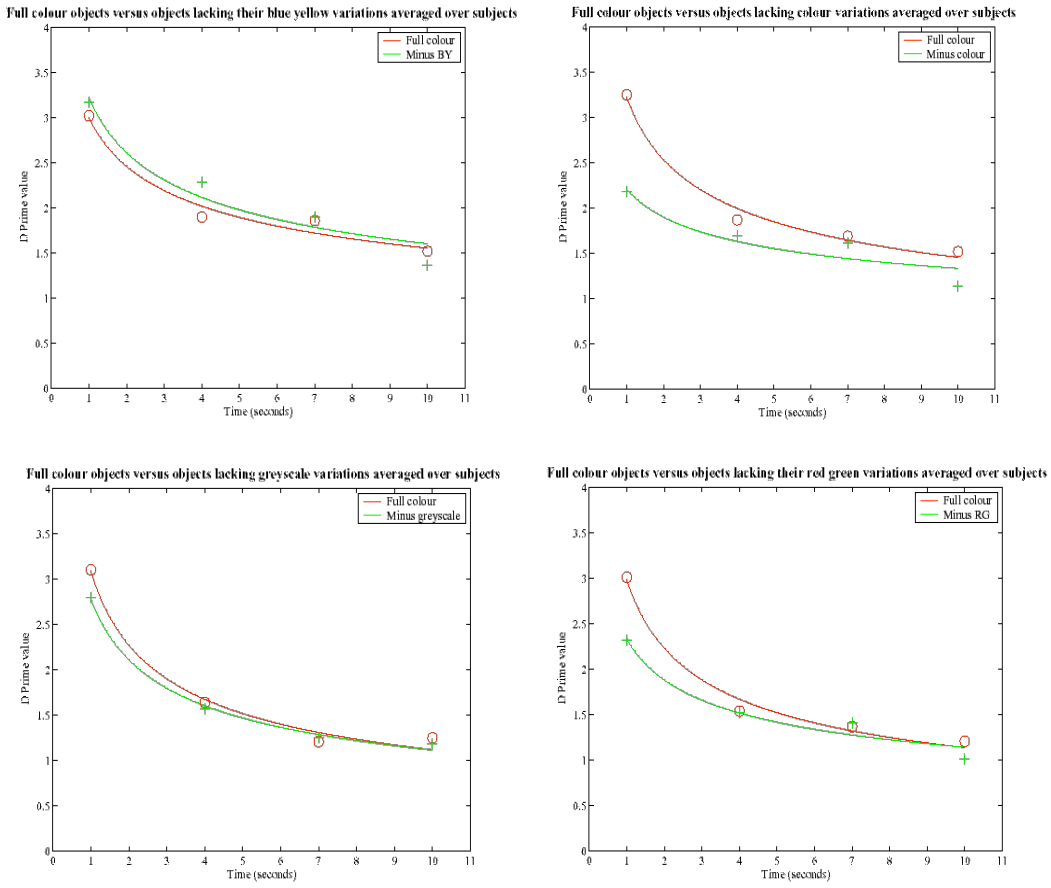

Figure 4-2: Curve fits relating to performance relating to the chromatic manipulations in each of the experimental groups.

Table 3: Parameters values for the curve fits shown in figure 6. Values are given for each group and stimulus type. *a* and *b* refer to the parameters in equation 2. FVE value refers to Fraction of variance explained by the fitted curve.

Group	Colour	*a*	*b*	FVE
Full colour v minus colour	Full colour	3.0631	0.3489	0.9936
Full colour v minus colour	Minus colour	2.2170	0.2570	0.9065
Full colour v minus GS	Full colour	3.0857	0.4404	0.9880
Full colour v minus GS	Minus greyscale	2.7796	0.3964	0.9960
Full colour v minus RG	Full colour	2.9839	0.4179	0.9878
Full colour v minus RG	Minus red-green	2.3340	0.3098	0.9604
Full colour v minus BY	Full colour	3.0001	0.2853	0.9725
Full colour v minus BY	Minus blue-yellow	3.2248	0.3034	0.9399

The curve fits show a similar pattern to that shown by the ANOVA. For objects lacking colour, or red-green colour, a marked decrease in the discrimination scores is apparent (particularly at the first delay interval) compared to full colour objects. For stimulus types containing no luminance modulation or no blue-yellow colour there is a subtle drop, no drop or facilitation in discrimination scores compared to full colour objects.

In order to examine the magnitude of effects at the first delay interval, separate t-tests were run on the two groups of data. These post hoc tests were based on the a –priori assumption that chromatic signals will be utilised by the visual system at early delay intervals but not at later delay intervals.

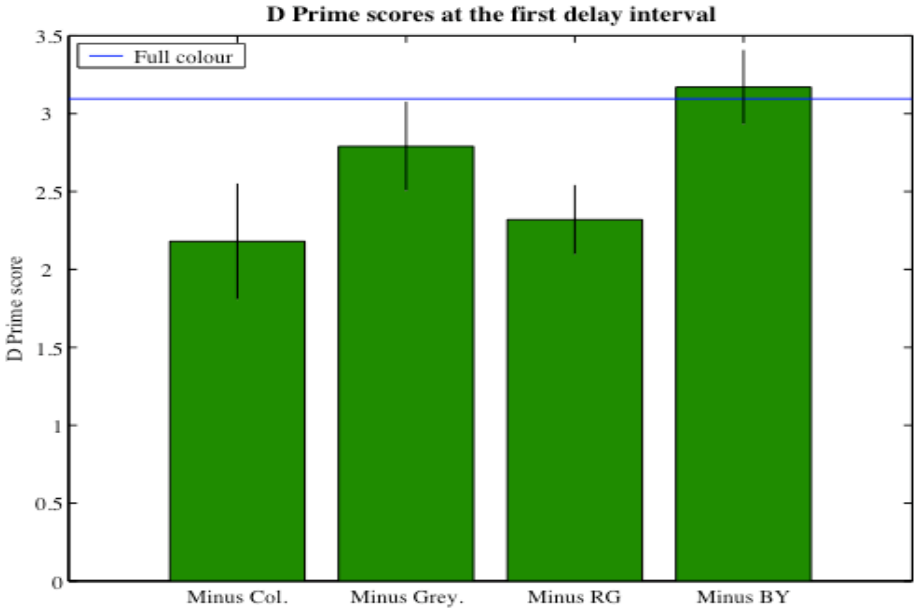

Figure 4-3: Discrimination scores for each stimulus manipulations, at the first delay interval. Data averaged over subject and session. Blue line shows the discrimination score (at the first delay interval) for full colour objects averaged across all groups.

Analysis of discrimination scores at the first delay interval revealed a significant difference between colour stimuli and stimuli lacking their green colour ($t_9 = 3.02$, $p < 0.05$). Subjects provided significantly higher d prime scores with objects containing full colour (mean = 3.01) than with objects containing no red-green colour (mean = 2.32).

At the first delay interval subjects provided significantly higher scores with full colour objects (mean = 3.25) than with objects lacking colour (mean = 2.18). No significant difference was observed for the group comparing full colour objects with objects lacking luminance modulation ($t_9 = 1.612$, p. = 0.141).

A significant difference was observed at the first delay interval in the group comparing full colour objects with objects lacking their colour ($t_9 = 4.282$, $p < 0.01$). Subjects performed significantly better with full colour objects (mean = 3.01) than with objects lacking colour (mean = 2.32)

For the group comparing full colour objects with objects lacking their blue-yellow components no significant difference was observed at the first delay interval ($t_9 = -0.555$, p. = 0.593). These data are shown in Figure 4-3.

4.3.4 Measures of reaction time across delay interval

In order to assess whether delay interval had a differential effect on reaction time across stimulus type, separate factorial ANOVAs were run on the data relating to each of the stimulus types, over changes in delay interval.

Main effects of delay interval on reaction time were found for Colour stimuli ($F_{3,27} = 3.106$, $p < 0.05$, $\eta^2 = 0.257$, $\delta = 0.658$) and minus luminance stimuli ($F_{3,27} = 2.930$, $p < 0.05$, $\eta^2 = 0.227$, $\delta = 0.637$) (See Table 4 and Table 5). Bonferonii corrected pairwise comparisons revealed no significant differences between delay intervals for these classes of stimuli. Increasing delay interval therefore had an effect on the reaction time provided by subjects. This effect did not correspond to the effects of stimulus manipulation.

Table 4: Mean Response time (in seconds) for each of the delay intervals for colour stimuli. Delay interval 1 = 1s, delay interval 2 = 4s, delay interval 3 = 7s, delay interval 4 = 10s. Data averaged over subject and session.

	Mean	Std. Error	95% Confidence Interval	
Delay			Lower Bound	Upper Bound
1	0.912	0.061	0.774	1.050
2	0.953	0.106	0.712	1.194
3	1.192	0.064	1.046	1.337
4	1.045	0.064	0.901	1.190

Table 5: Mean Response time (in seconds) for each of the delay intervals for minus luminance stimuli. Delay interval 1 = 1s, delay interval 2 = 4s, delay interval 3 = 7s, delay interval 4 = 10s. Data averaged over subject, session and stimulus type.

	Mean	Std. Error	95% Confidence Interval	
Delay			Lower Bound	Upper Bound
1	1.029	0.080	0.849	1.209
2	1.082	0.080	0.902	1.263
3	1.159	0.091	0.953	1.365
4	1.114	0.104	0.879	1.349

In summary, irrespective of the chromatic / luminance properties of the stimulus, increasing delay interval reduced discrimination performance. For full colour objects and objects lacking luminance modulation, increasing delay interval also increased the time subjects took to provide a response. Interactions with the main effects of delay and colour / red-green colour removal suggested that the difference between means was maximal at earlier delay intervals. This was made apparent with Bonferonii corrected pairwise comparisons and curve fitting techniques. Separate t-tests revealed the extent of the effects at the first delay interval and showed the same pattern that was observed with the main effects.

4.4 DISCUSSION

4.4.1 Overview of the results

There are two colour effects in the data. First performance with greyscale objects and objects lacking red-green colour modulation is impaired compared to performance with full colour objects. This shows that colour and potentially red-green colour channels make a distinct contribution to object recognition. Provided colour is present, neither luminance nor blue-yellow colour appears to be important. Second there is an interaction between the deficit observed from the removal of colour or red-green colour and the decay in recognition performance caused by testing objects at increasing delay intervals. This results in the following three points for discussion.

4.4.2 The possibility of confounding effects

It is possible to discount colour based effects as being caused by differing contrast sensitivity functions of the studied mechanisms. The chromaticity and luminance of the tested objects were based upon subjects' discrimination thresholds, measured independently for each of the chromatic and luminance mechanisms. Stimuli were therefore equated for in terms of chromatic and achromatic contrast and intensity.

Despite differences in the contrast sensitivity and acuity levels of the chromatic mechanisms and achromatic mechanisms (Kelly, 1983, Mullen, 1985), research exists to suggest that chromatic mechanisms can reach hyper acuity levels (less than 2 arcmin of visual angle), (Mullen and Beaudot, 2002).

Similar results have also been found in studies of vernier acuity. Measurements of detection thresholds with Gabor patches have shown no apparent difference between

achromatic and chromatic thresholds (Krauskopf and Farell, 1991). It is therefore possible to discount an explanation of the differences found in this study as a consequence of differences in acuity of the various visual mechanisms.

It seems unlikely that effects could be due to the state of adaptation of the subjects' eyes. Experiments were performed under dim room lighting, with stimuli rendered on a mid grey background. Subjects would have used the same photopic system that is used in a naturalistic day light environment.

A final consideration was that the subjects were using verbal techniques to memorise the stimuli. Although this possibility can not be excluded, the nature of the stimuli and the time course of the experiment make it very unlikely. The stimuli were trial unique and designed to have no explicitly nameable features. The time course of the experiment required subjects to constantly make a response, every three seconds. This would have made it hard for subjects to develop techniques or strategies to learn stimuli.

4.4.3 The removal of stimulus colour impairs recognition ability

The 25% decrease in discrimination scores caused by the removal of stimulus colour compares with the 5-10% decrease found by Wichmann and colleagues using natural scenes. The differences between these values could be as a result of differences in paradigm or stimulus (or both).

Although other studies have found that subjects also respond faster with colour stimuli (Wurm et al., 1993), I failed to find this effect. However, a slight drop in reaction times was shown for stimuli containing chromatic modulation compared with stimuli lacking chromatic modulation.

Speculations concerning the functional role of the chromatic and achromatic mechanisms are important as they provide a degree of insight into the function of colour as stimulus component. Some studies place emphasis on colour providing a sensory advantage to object recognition, others place a greater degree of emphasis on the diagnostic ability that colour provides. If stimulus chromaticity does not interact with the high resolution achromatic representation of the visual world, then presumably its role would be implicated in higher level diagnostic mechanisms. Based on the fact that our stimuli were designed not to rely on these types of mechanism, and the fact I got effects of colour removal, it seems likely that colour does indeed have a sensory role (although this could be attributed to higher level non diagnostic process'). This has been reported by several other studies. The structural representation of the visual input has also been shown to have an effect on perceived colour (Shady and MacLeod, 2002)

4.4.4 The selective effect of the removal of red-green colour

I found a 14% drop in discrimination performance as a result of removing red-green colour (compared to performance with full colour objects). Studies of shape discrimination that employ isoluminant chromatic stimuli based on the cardinal directions of colour space show the red-green opponent mechanism as performing better at shape discrimination than the blue-yellow. The relative drop in performance of 15% between red-green and blue-yellow stimuli observed adds weight to the preferential role of the red-green mechanism in object recognition.

The selective deficit in recognition found by removal of red-green colour suggests that the mechanisms implicated evolved specifically for the purpose of object recognition. This argument (summarised by Allen's hypothesis) states that primate

colour vision and the reflectance functions of the fruit which they consumed co-evolved providing advantage to both agents.

The fact that the red-green pathway evolved specifically for the purpose of object recognition, could also account for the lack of effects using colour deficient dichromat subjects. The task used by Gegenfurtner was one involving the recognition of natural scenes. This task would rely on segmentation mechanisms, which could be supported by the blue-yellow opponent mechanism (presumably specialised for this task). Indeed dichromats report difficulties in object recognition tasks such as detecting fruit amongst foliage on trees or shrubs (Stewart and Cole, 1989).

The properties of the cells that relay visual signals in the opponent pathways also support the concept that they have different functional roles. The midget ganglion cells that draw input from L and M cones generally have small receptive fields (at the fovea a single L or M cone and show centre surround opponency (Goodchild et al., 1996). The bistratified ganglion cells have larger receptive fields and lack spatial opponency (Dacey and Lee 1994). Edges that are mediated by this system are described as fuzzy or ill defined (Libeman 1929). It seems completely plausible that the higher spatial resolution afforded by the midget ganglion cells provides the advantage in object recognition inhibited in this study.

Having established the above results in humans, I wanted to examine if a similar deficit in ability was caused by the subtraction of chromatic modulation in a non-human primate species. A wealth of information has been collected regarding the functional characteristics of several neuro-anatomical areas in non-human primate species. For this

reason it was of interest to find out whether the effects that were found in this chapter could be replicated in the macaque monkey. This is discussed in the following chapter.

Chapter 5 MEASURES OF MACAQUE LIST LEARNING FOR COLOURED OBJECTS AND OBJECTS LACKING LUMINANCE RED-GREEN AND BLUE-YELLOW CHROMATIC INFORMATION

Experimental questions

Does the restriction of the chromatic modulation present within objects impede the ability to discriminate between objects?

Does the restriction of chromatic modulation conveyed along either of the two opponent pathways (red-green & blue-yellow) have differing affects upon object discrimination ability?

Is macaque list learning ability constant over changes in object composition, is this dependent upon the chromatic content of the discrimination pairs?

5.1 INTRODUCTION

It has been demonstrated that macaque monkeys show an ability to acquire large sets of object discrimination pairs, comparable to human subjects (Ringo et al., 1986). In their study Ringo and colleagues showed that two macaque monkeys recognised 79% and 85% of previously presented pictures. Human subjects working on a comparable task recognised an average of 83% of pictures.

In the present study measures were taken of the extent to which the chromatic properties of stimuli affected the ability of macaques to discriminate between pairs of objects. I investigated the degree to which chromatic restrictions inhibited list learning, with the intention of assigning a functional role to object chromaticity and assessing the contribution of different visual factors in list learning behaviour.

Relatively few studies have compared macaque discrimination ability for objects containing no chromatic variations with objects that contain chromatic variations. In the few studies that have been conducted in this area inconsistent results have emerged concerning the functional role of colour. In a categorisation task where monkeys were trained to classify photographs as either animal or non-animal, or food or non-food, no decrement was observed in accuracy or reaction time between images presented in colour or in greyscale (Delorme and Fabre-Thorpe, 1999). However, in a follow up study using a similar task and methodology a small mean RT increase (10-15ms) was observed for the classification of black and white stimuli depicting food items (Delorme et al 2000). As chromatic information in the P stream reaches visual cortex about 20ms after the M pathway inputs (Nowak et al., 1995), Delorme and colleagues suggest that

chromatic cues are only important when achromatic cues are sufficiently impoverished that a discrimination cannot be made.

These findings contrast with evolutionary and computational accounts that suggest that stimulus chromaticity is beneficial in object segmentation (Hurlbert, 1989, Mollon, 1989). Although the beneficial effects of colour have yet to be tested with non-human primates, studies with humans have shown performance to be impeded by colour subtractions using a variety of stimulus types (Gegenfurtner and Reiger, 2000, Wichmann et al., 2002). Further questions arise concerning whether the advantages in recognition are due to a richer representation in short term memory or an increased ability to segment the visual image. Recent work points to colour interacting with both (Gegenfurtner and Reiger, 2000).

Further questions arise when considering the functional relevance of specific types of chromaticity upon macaque perception. Macaque chromatic and achromatic contrast sensitivity have been shown to be very similar to humans (Merigan, 1989, DeValois et al., 1974). Macaque monkeys have trichromatic visual systems utilising cone types with similar spectral sensitivity to humans (Baylor et al., 1987). Questions arise concerning whether the differential effects of stimulus chromaticity (a deficit in performance [measured by radial modulation thresholds] for shape stimuli mediated by the blue-yellow system compared with the red-green system) found with object recognition in humans (Mullen and Beaudot, 2002) are also apparent with list learning in macaques.

Currently, no studies have investigated the differential effects of red-green and blue-yellow chromaticity upon macaque list learning. However a degree of insight can

be gained into possible effects by examining the neuronal basis of macaque chromatic processing. Early findings relating to the neuronal pathways responsible for conveying chromatic information suggested that red-green and blue-yellow chromatic information was commonly processed by the parvoceullar subcortical pathway (Derrington et al., 1984, Valberg et al., 1986). Toxicant-induced damage to this pathway has been found to disrupt chromatic sensitivity across cardinal and intermediate axis of colour space (Merigan, 1989). This would suggest a commonality between the red-green and blue-yellow chromatically opponent systems sub-serving visual discrimination.

Despite these findings, macaque contrast sensitivity functions show marked differences between the red-green and blue-yellow systems (Merigan, 1989). More recent research has suggested that a separate sub-cortical konioceullar pathway is responsible for carrying chromatic information to V1 (Hendry and Reid, 2000). Further differences in cyto-architecture between the photoreceptor types underpinning red-green and blue-yellow opponency add weight to the differing behavioural function of the opponent systems (see introduction). Studies at the level of the primary visual cortex also suggest that chromatic opponency is paired with spatial antagonism (Livingstone and Hubel, 1984). These results suggest that colour plays a low level role in the visual process, closely coupled with the spatial segregation of objects.

Investigations have also examined the degree to which the chromatic and structural properties of the visual representation interact. A number of studies have investigated the relationship between visual structure and chromaticity in macaque discrimination ability. Lesions of visual area V4 have been shown to cause deficits in both chromatic, pattern and orientation discrimination (Heywood and Cowey, 1987).

The similarity between deficits suggests a commonality in the mechanisms responsible for the processing of these independent stimulus attributes.

Other studies have focused upon the role of colour in memory. The medial temporal lobe memory system has often been implicated in visual object recognition memory (see introduction). Removal of various parts of inferior temporal cortex has been shown to disrupt colour discriminations (Cowey and Gross, 1970, Heywood et al., 1988, Merigan et al., 2000). Based upon impairments in these higher-level areas associated with perceptual-mnemonic function, speculation has arisen concerning the functional role of colour at a more abstracted level.

The balance of evidence therefore suggests that colour interacts with discrimination ability at a number of cortical levels. It remains a challenge for tasks designed to assess the functional role of colour to segregate these various mechanisms in order to find the function of chromatic information at various levels in the visual pathway.

In this study I sought to examine the behavioural relevance of stimulus chromaticity in macaque list learning. The macaques learnt 16 object discrimination pairs, based on the flower type objects detailed in the general methods. The objects were designed to require the use of perceptual mechanisms and not declarative mechanisms. They were therefore created with using several similar overlapping non-distinct ellipses. This meant that the objects contained a high level of feature ambiguity. The experimental task involved the monkeys reaching criterion (90% accuracy) on four lists containing four discrimination pairs. Each discrimination pair was produced so that the object contained:

chromatic and luminance variations or

luminance variations (achromatic objects) or

luminance variations and red-green chromatic variations (minus blue-yellow modulation) or

luminance variation and blue-yellow chromatic variations (minus red-green modulation).

The effect that either eliminating or restricting the chromatic variations present within an object had upon discrimination performance was examined. This was assessed using the mean percentage of correct responses that the monkey made whilst reaching criterion in a list and the number of errors produced whilst reaching criterion. Both of these indicators were used as a measure of ability in acquiring object discrimination pairs containing various amounts of visual information.

Based upon the findings in Chapter 4 , it was expected that, deficits in performance would be apparent for the subtraction of all chromatic information and red-green chromatic information, but not blue-yellow chromatic information.

5.2 METHODS

5.2.1 Overview of design

The list learning ability of macaques was tested using a two-alternative forced-choice methodology. In order to test the effects of chromatic restriction discrimination pairs of various chromatic specifications were used. Each monkey learnt four lists, each containing four discrimination pairs. Of the discrimination pairs, one pair consisted of objects that were unrestricted in their chromatic specification. One pair consisted of objects that contained no chromatic variations. One pair consisted of objects that contained no blue-yellow chromatic variations and one pair consisted of objects that contained no red-green chromatic variation.

5.2.2 Subjects

Two female rhesus monkeys (Macca mulatta) were used as subjects. The monkeys were housed in a communal group of three, and were provided with unrestricted amounts of water or sugar-free juice. The monkeys were fed on a diet of mixed fruit and universal diet. A small amount (< 20g) of foraging materials were available in the communal housing area daily.

Monkeys were weighed weekly. If their weight increased or decreased by over 10% over a successive number of weight measurements then their diet was altered. This did not occur during the time course of the experiment. During the experimental period Mildred weighed approximately 5 kg and Hyacinth weighed approximately 4.5kg.

5.2.3 Equipment

The monkeys performed the task using automated testing equipment. The equipment consisted of a Microtouch17 inch capacitive touch screen monitor housed in a movable trolley that was bolted to a wall. The monkeys sat in a raised movable transport cage that was attached to the touch screen trolley using lockable aluminium arms. The front end of the transport cage allowed the monkey to reach outside of the transport cage and touch the screen or collect rewards.

A food hopper was located below the central mid line of the screen, in to which 45mg sucrose or banana flavoured pellets were dispensed. The pellets were dispensed using a Med Associates automated pellet dispenser located on top of the monitor trolley, out of reach of the monkey.

The monitor was driven by a dual head Matrox Millenium G400 graphics card attached to a Pentium PC, equipped with 260 MB RAM. The windows desktop was set to 1600 by 600 pixels and output was split between two monitors. The first monitor was used to initiate and control the task, and also provided indications of the monkey's progress. The second of the two monitors was used to display the experimental task, and the output for this monitor was also split between two screens.

One of the screens that displayed the experimental task was located in a room adjacent to the testing room and was used by the experimenter to view the task progress. The other of these screens was the touch screen and interfaced with the PC's serial port. This was located in front of the monkey and was used by the monkey to provide a response. The touch screen phosphors and luminance output are provided in the appendices section 10.1.2.

The experimental software was run on Windows NT version 4 and was written in visual C++. It operated in a real time mode designed to prioritise the resources allocated to experimental software.

5.2.4 Procedure

The monkeys moved voluntarily from their communal housing area to individual cages shortly before the experimental session was due to commence. The experimenter attached the transport cage to the individual cage containing the monkey to be tested, and the monkey moved into the transport cage. The transport cage was then moved from the holding room into a separate testing room. The transport cage was attached to touch screen apparatus and the testing session commenced.

The experimental session consisted of 160 trials. On each trial two objects were placed on the screen centred at positions 250,250 (pixels) (L) and 550,250 (R). The objects differed in their structural properties and their chromatic properties. However, both objects were of the same chromatic class (chromatic, achromatic, lacking red-green variation or lacking blue-yellow variation). Objects were placed upon a grey background mid-level luminance.

Within each session of 160 trials, 40 of the trials were of each of the four discrimination pairs. For each discrimination pair, one of the objects was constantly rewarded (the positive object) and one of the objects was never rewarded (the negative object). The task was to learn to touch the rewarded objects in as many trials as possible in order to achieve the maximum reward. Left-right positions were randomised with equal numbers of positive objects placed on the left and right hand sides of the screen.

The positive object was assigned to the left or right hand side of the screen using a pseudorandom sequence, as was the colour condition that the object belonged to.

Trials lasted for up to 10 minutes, after which the trial was defined as a time out and the session ended. If the monkey pressed the positive object before this time then a reward was dispensed, the objects were removed from the screen, and an inter trial delay of 2 seconds commenced. If the negative stimulus was pressed then the objects were removed and a 5 seconds inter-trial delay commenced. When the monkeys reached criterion by making a correct choice in 90% of trials during a session for a given list, then the next session commenced containing objects from a new list.

5.3 RESULTS

5.3.1 Effects relating to the removal of chromatic modulation

The effect of the removal of chromatic modulation from objects was investigated by comparing discrimination ability with sets of chromatic and achromatic objects. It was expected that the removal of stimulus chromaticity would produce a deficit in the ability of macaques to learn discrimination pairs. This deficit would result in subjects producing an increase in the number of errors for achromatic discrimination pairs and a decrease in the overall percentage of correct responses for the acquisition of achromatic discrimination pairs.

The numbers of errors made for each condition were summed across sessions. The resultant value was obtained for each list and used as an indictor of the monkey's performance. Comparatively larger numbers of errors made prior to achieving criterion for a list indicated a decrement in performance for a particular condition.

A paired samples t-test revealed no significant difference between the total numbers of errors to criterion for chromatic (mean=35.625, SEM = 23.8) and achromatic objects (mean=46.625, SEM 16.5) (t_7=1.049, p = 0.329) (A similar pattern of results was observed when using the mean percentage of correct responses for lists). The lack of significance between the seemingly different means was due to the high level of variability within the experimental data.

Under some conditions monkeys still produced errors for a particular discrimination pair, after they had reached criterion for that stimulus pair. For example, if criterion was achieved for a chromatic discrimination pair in session 5, and criterion

was achieved for the list in session 10, errors could still have been produced for colour object pairs between sessions 5 and 10).

In order to discount any effects relating to this type of behaviour, a similar analysis was performed that discarded errors made for a stimulus pair after criterion was reached (for that pair). No differences were found between chromatic (mean=12.385,SEM = 4.34) discrimination pairs and achromatic discrimination pairs (mean =30.625,SEM=19.75) ($t_7 = 0.734$ $p = 0.487$).

To further quantify the relationship between chromatic and achromatic objects, the number of errors made within each session were examined. These are shown in Figure 5-1. Each point represents the comparative number of errors made within a session for chromatic and achromatic objects. Points were taken for each session performed by the two monkeys, for each list. A weak linear relation ship was observed between variables ($r = 0.427$), the majority of points plotting in the section of the chart where more errors were made for objects lacking chromaticity (mean = 7.4902 sd = 6.7) than colour objects (mean = 5.5882 sd = 5.5).

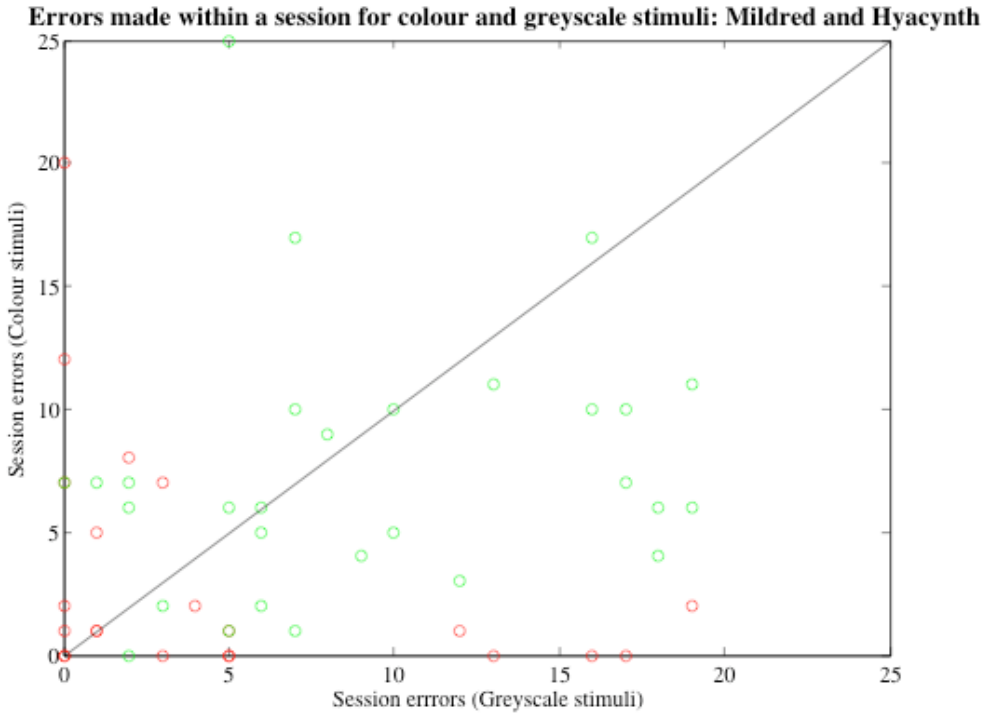

Figure 5-1: The number of errors within each session for each monkey on chromatic and achromatic discrimination pairs. Diagonal represents similar performance on both types of object. Green circles = data from Mildred; Red circles = data from Hyacynth

A measure was also calculated of how many errors were made in the various chromatic conditions, irrespective of changes in overall performance. The fractional error was calculated using the following equation:

Equation 12

$$E_F = E_C / E_S$$

In Equation 12, E_C represented the number of errors made in one condition by one monkey performing one session, and E_s represented the number of errors made over all conditions by one monkey in one session.

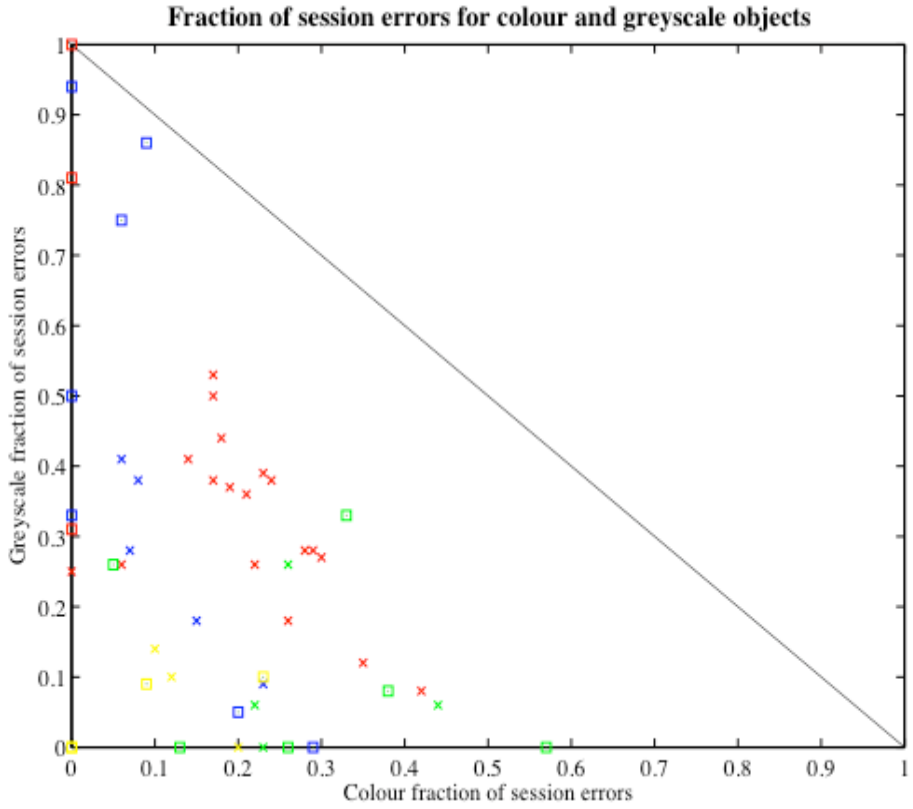

Figure 5-2: The fraction of errors produced for chromatic and achromatic objects when compared to the total number of errors within a session. Crosses represent data from Mildred. Squares represent data from Hyacynth. Points can only plot in bottom half of figure (indicated by diagonal). A fractional value of 1 indicates all errors were in a specific condition.

When data were compared using the session number as a within subjects variable, a significant difference was found between ratios for chromatic (mean=0.173) and achromatic objects (mean=0.2830) ($t_{50} = 2.352$ $p<0.05$). This trend is shown in Figure 5-2 where it can be seen that the ratio of condition specific errors to total errors was generally found to be greater for achromatic objects than chromatic objects.

This result suggests that when the overall level of performance within a session is factored out, a difference can be observed in the tendency to make errors on greyscale

objects, compared to colour objects. Although the time course of learning a discrimination pair is not affected by the removal of stimulus chromaticity, the tendency to make errors within a session is.

Further analysis was conducted in order to establish whether the decrement in performance found for achromatic objects also existed in reaction time data. Mildred provided significantly faster responses for chromatic object than achromatic objects (t_{29} = 2.493 p = 0.019). This difference was not apparent for Hyacynth (t_{20} = 1.049 p = 0.307) (Mildred Normal objects RT mean = 1386.93ms SEM = 68.74, Greyscale (achromatic) objects RT mean = 1524.29ms SEM = 78.39), (Hyacynth Normal objects RT mean = 3155.03 SEM = 96.98 , Greyscale objects RT mean = 3319.09ms SEM = 136.19).

In summary comparison of list learning performance for chromatic and achromatic object pairs revealed no difference in the number of errors made whilst learning discrimination pairs. There was also no difference found for the mean hit rate (or average percentage of correct response) associated with the learning of the two types of discrimination pair. When the ratio of condition specific errors to the number of errors made within a session was calculated then a difference was observed between chromatic and achromatic objects. This suggested that when the overall performance within a session was discounted then a difference existed between the tendency to make errors with chromatic and achromatic discrimination pairs.

5.3.2 Effects of removing red-green chromatic modulation versus blue-yellow chromatic modulation.

In order to further quantify the effect of chromatic subtraction, two additional classes of objects were tested that contained no variations in red-green chromaticity or no variations in blue-yellow chromaticity. These objects were tested in order to establish whether deficits observed for achromatic objects generalised to the removal of either red-green colour or blue-yellow colour. It was expected that the removal of red-green colour would cause a deficit in visual performance that would not be observed with the removal of blue-yellow colour. This would be apparent by a lower mean percentage of correct responses for objects lacking red-green colour compared to colour objects.

The errors made in achieving criterion for discrimination pairs of all chromatic specifications were compared. Statistical analysis was performed using a single repeated measures ANOVA. The 4 chromatic conditions (chromatic, achromatic, minus red-green and minus blue-yellow objects) were defined as a within subjects factor. The successive lists were assigned to a between subjects factor. Attributing the successive lists to a between subjects factor has been used in other studies of macaque list learning (Bussey et al., 2002). No effects of colour manipulation or list number were found (colour : $F_{3,12} = 2.808$ $p = 0.085$, $\eta^2 = 0.412$, $\beta = 0.526$, list: $F_{1,4} = 5.520$, $p = 0.079$, $\eta^2 = 0.580$, $\beta = 0.434$).

Analysis was also conducted using a measure that discounted errors made within a condition after criterion was reached for that condition. A similar pattern of results was observed (colour: $F_{3,12} = 1.515$ $p = 0.261$ $\eta^2 = 0.275$, $\beta = 0.302$. list: $F_{3,12} = 2.186$ $p =$

0.103, $\eta^2 = 0.621$ $\beta = 0.608$). In summary no differences in the numbers of errors made in reaching criterion were apparent for any of the chromatic manipulations.

The number of errors produced in achieving criterion for a list was an adequate measure of performance used by many studies of macaque list learning. However, it was sensitive to variations in behaviour when lists were acquired quickly and performance was not consistent. The average proportion of correct responses (hit rate) taken over all sessions was less sensitive to session based performance deviations. This was because data was averaged and not summed. If the monkeys were subject to changes in motivation then the averaging over sessions factored out outlying data points, and provided a clearer overall measure of the monkeys performance.

Analysis was also conducted upon the mean hit rate for each list. A main effect of stimulus chromaticity was found ($F_{3,12} = 3.632$ $p < 0.045$). No main effect of list number was found ($F_{3,4} = 3.540$ $p = 0.127$). Pairwise comparisons revealed a significant difference between the mean hit rate for colour objects (mean = 0.879 SEM = 0.026) and objects lacking blue-yellow colour modulation (mean = 0.791 SEM = 0.017), a similar deficit was observed with objects lacking all chromatic modulation (mean = 0.782 SEM = 0.034).

Although there was no difference in the number of errors made in reaching criterion, there were differences in the mean percentage of correct responses made for each of the discrimination pairs. When performance with objects lacking red-green chromatic modulation was compared to performance with objects lacking blue-yellow chromatic modulation a reasonably strong correlation was observed ($r = 0.676$), suggesting that levels of performance within the conditions were linearly related. This is

shown in Figure 5-3, where the majority of points plot near or around the main diagonal. The high level of correlation observed for these conditions and the similar statistical differences suggest that deficits in performance are common to both red-green and blue-yellow colour subtractions.

When ratios were calculated using Equation 12, repeated measures ANOVA revealed a similar trend to the results found with the hit rate. Data was not found to meet the assumptions of ANOVA ($W_5 = 0.532$ $p = 0.000$). A Greenhouse-Geisser correction to the degrees of freedom was therefore applied. A significant main effect of chromatic manipulation was found ($F_{2.255,105.99} = 7.645$, $p < 0.01$) alongside a significant interaction between colour and list number ($F_{6.765,105.99} = 5.181$ $p < 0.001$). Bonferonii corrected pairwise comparisons revealed significant differences at the $p<0.001$ level between colour objects (mean=0.171 SEM = 0.018) and objects lacking blue-yellow colour (mean=0.3 SEM = 0.027) or red-green colour (mean=0.296 SEM = 0.020).

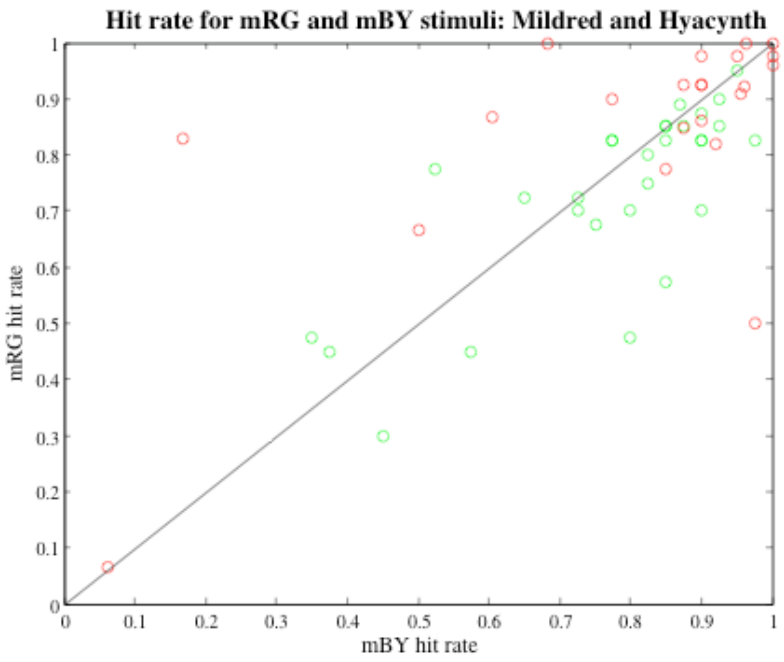

Figure 5-3: Chart of the hit rate for object pairs lacking red-green and object pairs lacking blue-yellow colour. Each point represents the comparative performance for objects of the two chromatic classes. Points provided for each monkey's performance within each session. Points on diagonal show no differences between performance with objects from the two chromatic classes. Green circles = data from Mildred; Red circles = data from Hyacynth

5.3.3 Effects of subject response times

In order to further quantify differences in response characteristics between the experimental groups, mean reaction time value was calculated for each of the groups within each of the sessions. Data was found to be normally distributed ($W_5 = 0.817$ $p = 0.134$). A repeated measures ANOVA revealed a significant main effect of the stimulus condition ($F_{3,129} = 3.382$, $p < 0.05$, $\eta^2 = 0.073$, $\beta = 0.754$) and monkey ($F_{1,43} = 259.62$, $p < 0.001$, $\eta^2 = 0.976$, $\beta = 1$).

Bonferronii corrected pairwise comparisons revealed a significant difference between mean RT for full colour objects and object lacking red-green chromatic information $p < 0.05$). Both monkeys provided significantly faster responses for full colour objects compared with objects lacking red-green information (Mildred FC mean = 1386.9 SEM = 68.74 , minus red-green mean = 1536.5 SEM = 84.96; Hyacynth FC mean = 3155.0 SEM = 96.98, minus red-green mean = 3473.1 SEM = 112).

Data were also analysed for the first session that the monkeys performed in for each list. It was hoped that by examining the earliest point in the time course of acquisition, the visual contribution to the discrimination of object pairs could be examined. Analysis was performed upon the hit rate for the various chromatic conditions. This measure was used as there was no need to correct for the level of overall session performance (as data was only taken from the first session).

Statistical analysis revealed a main effect of object chromaticity ($F_{2,8} = 7.205$ $p = 0.016$, $\eta^2 = 0.643$, $\beta = 0.801$). Pairwise comparisons, significant at the $p < 0.05$ level, revealed that the monkeys provided a significantly lower hit rate for object pairs lacking red-green colour (mean= 0.473) than for full colour objects pairs (mean=0.716). This significant difference was not observed for objects lacking blue-yellow colour (mean=0.580). The removal of red-green chromatic information caused a significant deficit in performance during the first session. This was not observed with the removal of blue-yellow chromatic information.

In summary differential levels of discrimination ability were found for objects lacking red-green and blue-yellow colour. These were present in reaction time data and performance levels in the first session. Deficits in performance were observed for the

mean list hit rate (percentage correct) and the fraction of errors made within a session for objects lacking red-green and blue-yellow information. However these deficits were common to objects lacking both red-green and blue-yellow colour. The finding of deficits in measures where list based learning has been factored out, either by taking a ratio or averaging over sessions, adds further weight to the concept that colour subtractions impede the processing of object based information, rather than the conceptual acquisition of object pairs.

5.3.4 The effect of object structure

Analysis was conducted on the effects that the object structure had upon measures of list learning ability. It was of theoretical interest to examine possible effects of object structure upon the measures of discrimination ability. Also of interest were any potential interactions between the presence of chromaticity and the role of object structure. It was expected that the type of object used would produce no structural based modulation in performance and this would be constant over changes in chromaticity.

Levels of performance for the acquisition of multiple sets of objects were compared. Objects differed in structural composition but remained constant in chromatic composition. Data were analysed using several one-way ANOVAs. A separate ANOVA was utilised for each chromatic condition (the list number being defined as a between subjects factor).

Data was found to meet the assumptions of ANOVA (Mauchly's $W_5 = 0.442$, $p=0.828$). Tests revealed no significant differences between list numbers (indicating changes in object structure) in three out of the four chromatic specifications. This

implied that the changing object structure had no effect on overall performance for these conditions.

Analysis revealed that the monkeys provided a constant number of errors before achieving criterion (irrespective of changes in object structure) for full colour objects ($F_{3,7} = 0.450$ $p=0.731$), objects lacking red-green colour modulation ($F_{3,7} = 0.233$ $p=0.869$), objects lacking blue-yellow colour modulation ($F_{3,7} = 0.777$ $p=0.565$) but not objects lacking chromatic modulation ($F_{3,7} = 73.327$ $p <0.001$). Post hoc tests (Bonferonii corrected) revealed significantly different scores for the objects lacking chromatic modulation in Lists 1 and 2, Lists 1 and 4, Lists 2 and 3, and Lists 3 and 4.

A similar pattern of results was observed when using the average hit rate for each stimulus condition within each list. Constant performance was observed across changes in structure for full colour objects ($F_{3,4} = 0.724$ $p = 0.588$), objects lacking red-green modulation ($F_{3,4} = 0.360$ $p = 0.786$) and objects lacking blue-yellow modulation ($F_{3,4} = 4.455$ $p = 0.091$). Changes in performance were observed across list number for objects lacking chromatic variations ($F_{3,4} = 19.243$ $p <0.01$).

It was apparent that stimulus structure had no effect on macaque ability to learn objects that contained an unrestricted or partially restricted chromatic specification. For the objects that lacked all chromatic content, structural content produced a greater (significant) variation in performance.

Structural effects were found for measures of discrimination ability based upon achromatic objects, but not chromatic objects. This suggests that the structural properties of the objects are important when chromatic information is removed from an object.

Therefore, the type of information used to perform discrimination is dependent upon the range of information present within an object.

5.4 DISCUSSION

A significant increase in the likelihood of making errors was observed for achromatic objects. Differences in reaction times were also observed between chromatic and achromatic objects.

When chromaticity was selectively removed from discrimination pairs, differences were found between performance levels for normal and chromatically restricted objects. These impairments were common to objects lacking red-green information and blue-yellow information.

A significant deficit (compared to performance with full colour objects) was found in the hit rate taken within the first session for objects lacking red-green colour. This was not found for objects lacking blue-yellow colour. A significant increase in reaction time was also observed for objects lacking red-green colour compared with full colour objects. This was not observed with objects lacking blue-yellow chromatic modulation. Results also showed that the structural properties of the discrimination pairs had no effect on performance other than with achromatic objects.

Motivational factors could have affected the rate of list based acquisition, but as the monkeys were tested using a within lists design, this should not have biased the acquisition of specific discrimination pairs. Finding differences in the number of errors to criterion but not in the mean percentage of correct responses, suggests that differences between the conditions were in the shape of the acquisition curve.

Effects relating to the subtraction of object chromaticity were only found using a index of the ratio of errors made for achromatic objects to errors made within the

session. The advantage of using this measure was that the overall performance within a session was factored out. This allowed analysis using each session as a within groups variable, rather than each an average for each list. The resultant statistical analysis was more powerful, as it involved less averaging of data.

It cannot be discounted that the lack of an effect observed using measures that averaged over session were due to low statistical power. In this case an effect could be present but was not expressed using the framework that was employed. The scatter plot of errors made within a session for colour and greyscale discrimination pairs seems to concur with this possibility, the majority of points plotting in a region of the graph that would suggest an increase in the tendency to make errors for greyscale objects.

Where other studies have examined the effect of removing stimulus colour in macaque discrimination tasks, no effect has been found (Delorme and Fabre-Thorpe, 1999). However the lack of effect in this study may relate to the conceptual nature of the task (classifying objects as animal or non animal). Where the task has relied upon identification (in this case the kingfisher bird), drops in performance have been observed when pictures were presented in black and white (Roberts and Mazmanian, 1988). Similar results have been found with human subjects, colour being shown to provide an advantage in recognising a variety of stimuli (Wichmann et al., 2002, Tanaka et al., 2001, Shepard, 1967).

The finding of selective chromaticity effects for data from the first session, but not for data averaged over the time course of acquisition suggests a visual processing account of the results. This converges with the results from Chapter 4 , where selective effects were only found at short delay intervals that required a minimal memory

involvement. Psychophysical studies have shown that the macaque chromatic contrast sensitivity is modulated by changes in the spectral properties of light, and is similar to that of humans (DeValois et al., 1974). Therefore arguments relating to the compensations made using the threshold scaled objects proposed in Chapter 3 and Chapter 4 also apply to these findings.

Although no laboratory studies of visual perception have addressed the differential role of colour in the macaque monkey, a great deal of speculation surrounds the functional role of the red-green chromatic discrimination unique to old world primates. Examples of how chromatic cues can produce a perceptual pop-out effect useful for the detection of fruit amongst foliage have been proposed (Regan et al., 1998). Further work has suggested that this effect may be based upon the selection of ripe leaves (Lucas et al., 1998) in both cases, trichromatic vision is modulating behaviour in a way that dichromatic vision can not.

Despite various evolutionary accounts of differences in the functional role of red-green and blue-yellow chromaticity, studies that disrupt chromatic processes have failed to find any differential effects. Lesions of retinal-geniculate, striate (V1) and extra-striate (V4) processes have produced a global deficit in chromatic discrimination (Heywood and Cowey, 1987, Merigan, 1989). Apart from one recent study in V2 (Xiao et al., 2003), studies have failed to find structural segregation between cortical cells that are selective for red-green colour or blue-yellow colour. In fact, there is a degree of debate concerning whether cells that differentiate between red-green and blue-yellow colour are found in cortex (see introduction). A comprehensive neurological framework capable of supporting accounts of differential function for red-green and blue-yellow

colour has therefore yet to be proposed. However the fact that differential effects were found in this study suggests that some form of dichotomy exists between the two chromatic systems at a perceptual level.

The independence of the neuronal processing of chromatic cues and structural cues has also been examined by a number of studies. Based upon the segregation of input from the P and M pathways it was proposed that there was a specific system within visual cortex devoted to the processing of colour (Livingstone and Hubel, 1988). Such views contrast with other studies that fail to find anatomical segregation between cells selective or unselective for colour (Leventhal et al., 1995). In this experiment changes in object structure did not affect chromatic objects, but did affect achromatic objects. This suggests a degree of segregation between chromatic, achromatic and structural processing

In V1 chromatically responsive cells were found to be capable of encoding the spatial properties of the stimulus (Lennie et al., 1990). In V2, most chromatically responsive cells are selective for colour and structure (Gegenfurtner et al., 1996). These findings suggest that attributes relating to colour and form are processed concurrently. In light of these findings it seems more probable that the differences observed between the role of structure in objects containing achromatic and chromatic cues are a result of the reduction of the visual information available, rather than an indicator of separate processing systems.

The next chapter examines effects of the subtraction of stimulus chromaticity in a new world monkey. The advantage of the marmoset species is that animals have either dichromatic or trichromatic vision. I wanted to assess the function of stimulus colour in

a dichromatic species as this would allow an informative comparison with the results found in trichromatic species.

Chapter 6 MEASURES OF MARMOSET VISUAL DISCRIMINATION ABILITY FOR CHROMATIC AND ACHROMATIC OBJECTS

Experimental questions

Does the removal of chromatic modulation impede the ability of marmosets to acquire discrimination pairs?

Does the contrast of chromatic or achromatic objects affect the ability of marmosets to acquire object discrimination pairs?

Is performance constant over changes in object structure?

6.1 INTRODUCTION

Chromaticity (colour) has been shown to provide a sensory and a coding advantage for object recognition in human and non-human primates (see Chapter 1 , Chapter 4 and Chapter 5). In trichromatic species two sub-cortical pathways originating in the retina, convey chromatic information (see introduction).

It has been suggested that the red-green pathway mediates the advantage provided by the presence of chromaticity within objects (Mollon, 1989). This chromatically opponent pathway is present within trichromatic but not dichromatic visual systems. If such an advantage is unique to trichromatic vision, then it would be expected that the removal of stimulus chromaticity would have no effect on the performance of dichromatic subjects.

In a study with X-chromosome linked dichromats it has been found that the advantage afforded by colour is common to dichromatic and trichromatic visual systems (Gegenfurtner et al., 1998). The authors conclude that the human dichromat subjects may compensate in some way for the reduction in their chromatic ability and are therefore not impeded when stimulus chromaticity is removed. This finding contrasts with more subjective accounts of the difficulties that colour blind subjects experience (Stewart and Cole, 1989).

Questions remain concerning whether such a compensation is unique to human subjects. More specifically, are non-human primates with dichromatic visual systems impaired when chromatic information is removed from objects? A resolution of this question could suggest whether the advantage that chromatic information plays is unique

to the trichromatic visual system or whether the primordial blue-yellow opponent pathway unique to a subset of new world monkeys also contributes to the advantage that colour affords.

The common marmoset (Callithrix jacchus) has been used to test theories of dichromatic and trichromatic function. Marmoset populations are polymorphic in terms of their colour vision abilities. All males and homozygous females are dichromats. All heterozygous females are trichromats (Jacobs, 1993). Microspectrophotometry studies have shown that the homozygous marmosets utilize one of three long wave photoreceptor pigments at 563-567 nm, 556-559 nm and 543-545 nm along with a short wave cone type of around 433nm (Travis et al., 1988). The elaborate variability in the types and number of photoreceptor present within marmosets make it an interesting and powerful species for the study of chromatic ability.

The general chromatic discrimination abilities of marmosets have been addressed by a number of laboratory studies. Marmosets have been shown to be capable of discriminating between chromatic and achromatic images (Derrington et al., 2002). In this study the animals discriminated on the basis of colour as a stimulus attribute, rather than by learning a list of colours. The authors concluded that colour was of behavioural salience for the animals.

Other studies have shown that chromatic processing is impaired in dichromatic marmosets compared to trichromatic marmosets. In a study investigating marmoset foraging ability, researchers found that trichromatic marmosets found a significantly greater number of orange but not green cereal balls than did dichromatic marmosets (Caine and Mundy, 2000). Spectral modelling studies have also showed that dichromatic

visual systems are at best impaired when discriminating naturalistic fruit from foliage (Regan et al., 1996, Osorio and Vorobyev, 1996) Based upon these findings it would be tempting to conclude that the dichromatic visual system provided little or no chromatic advantage in object recognition tasks.

This viewpoint is further confirmed when evidence concerning the function of the more recently evolved red-green chromatic pathway is considered. Trichromatic visual systems can be advantageous in detecting certain types of fruit amongst foliage under various types of illumination (Regan et al., 2001). Other researchers have suggested it as being important for detecting ripe from unripe leaves (Dominy and Lucas, 2001). Despite these findings it has also been shown that dichromats are able to discriminate a great variety of ripe from unripe fruit (Sumner and Mollon, 2000).

Further to the study of Sumner and Mollon, various functional advantages have been attributed to dichromatic colour vision. Dichromatic vision has been suggested to be advantageous in allowing the breaking of camouflage (Anonymous, 1940, Morgan et al., 1992). It has also been shown that dichromaticity affords greater spatial resolution due to the nature of the photoreceptor mosaic (Williams et al., 1991). Both of these abilities would facilitate the recognition of objects within naturalistic environments. The comparative function of the single blue-yellow pathway present in dichromats and the additional red-green pathway present in trichromats therefore remains an area for investigation.

Comparison of the role that chromaticity plays in trichromatic and dichromatic vision is of benefit as it provides insight into the function of colour in the visual system. Previous findings have established that removal of stimulus colour impedes

discrimination ability in trichromatic subjects. In this study I intended to compare these effects in dichromatic subjects by measuring discrimination ability for chromatic and achromatic objects. If the removal of stimulus colour has an effect on dichromatic visual recognition, then the primordial blue-yellow system must be using the chromatic content of an object to facilitate recognition. Results of this nature would allow comparison between the functional properties of dichromatic and trichromatic vision.

To test this hypothesis four male dichromatic marmosets were trained to discriminate between rewarded and unrewarded flower-like object stimuli. Objects were produced that contained chromatic and luminance modulation along with objects that contained only luminance modulation. By comparing the ability to discriminate between objects of these types it was possible to assess the extent to which the dichromatic visual system relied upon chromatic cues.

In order to ensure that differences in behaviour were a product of stimulus chromaticity rather than stimulus contrast, both types of objects were presented at high and low contrast. It was expected that this manipulation would have no effect on behaviour. Consideration was also given to the effect that changing object structure had upon performance. In order to ensure that any differential effects observed were a product of the chromatic content of objects rather than the structural composition of the objects, performance was assessed across objects of the same chromatic content and the objects within each list were counterbalanced across monkeys. It was expected that the structural content of the stimuli would have no effect on behaviour.

6.2 METHODS

6.2.1 Subjects

Four male marmosets were trained in the study. The marmosets were housed in communal groups of three to four. The animals were housed in environmentally controlled conditions where temperature and humidity were held at optimum levels. Marmosets were fed their daily diet (marmoset chow, fruit and milk) after the testing sessions had been completed. The marmosets had constant access to water. Weights were continually monitored and if weight increased or decreased by more than 10% of their body mass then diet was reviewed.

The marmosets were moved from the communal housing areas to an isolated testing room using a small transport cage. The marmosets voluntarily moved from the communal cage into the transport cage. The transport cage was then placed within the testing apparatus and the marmoset got out into the testing equipment.

6.2.2 Equipment

The marmosets were tested in an automated Y Maze. The maze consisted of three arms interconnected by a central chamber. The arms and central chamber consisted of opaque sides and floor and a transparent ceiling. All parts of the maze contained removable rubber flooring. This was cleaned regularly in order to eliminate any form of scent. The end of each arm was open and a monitor was placed against the arm so that the marmoset could not leave the equipment. All of the monitors were visible from central chamber and were used to display the experimental stimuli.

Each arm contained 2 sets of infrared (IR) emitter detector pairs (RJ-E136302 US). These components emitted pulsed IR beams. The beams were directed across the arm, orthogonal to the sides of the arm. Reflective panels were positioned opposite to each emitter detector pair. The panels redirected the emitted IR beam back towards the IR detector. The resultant IR beam therefore traversed the Y Maze arm (Figure 6-1).

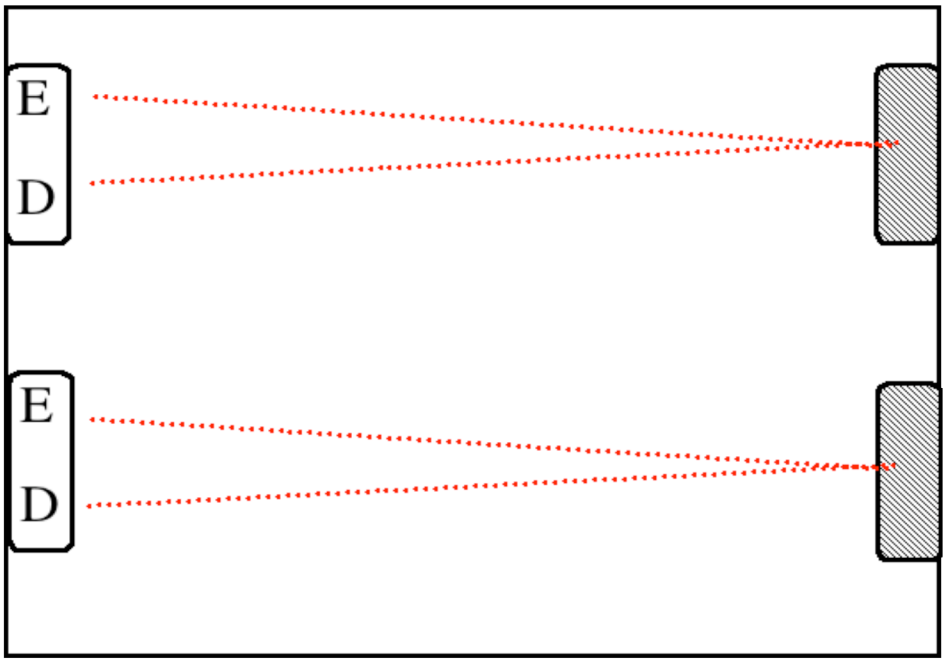

Figure 6-1: Section of a Y Maze arm. Left hand boxes (non hatched rounded boxes containing E and D) represent IR components. E = IR emitter, D = IR detector. Right hand boxes (hatched rounded boxes) represent reflector components. Dashed line represents IR beam.

Each Y Maze arm contained two IR beams. Both beams were positioned towards the end of each arm. The first of the two beams (the lower beam) was positioned above the floor of the Y maze. The second (the upper beam) was positioned below the ceiling of the Y Maze.

The IR detectors were connected to logic circuitry. When either the upper, lower or combination of upper and lower beams were broken a transistor to transistor logic (TTL) pulse was generated. This was sent to the control computer via shielded multi-wire cable. For each Y Maze arm a signal could be produced, representing one or both of the IR beams being broken at a given distance along the arm. In total there were 3 TTL 5V control signals (one for each the three arms), set to signal high on beam breaks.

At the end of each Y Maze arm, a food well was located. This well consisted of a hole cut into the floor of the maze, leading to a circular turntable. The circular turntable contained food hoppers and was rotated by a stepper motor controlled using a TTL pulse train. The motors could be initiated from the control computer or via inbuilt circuitry housed within the maze. Each arm contained one stepper motor / turntable system. The maze therefore contained 3 pulse train input lines.

The Y maze input output (IO) lines were connected to the screened multiwire cable using 3 RS 232 connectors attached to each Y Maze arm. The control computer interface consisted of a NI interface breakout box. The breakout box was connected to a NI DAQ card via ribbon cable. This system allowed the control of the various IO lines via NIDAQ C routines.

The task was run and the maze was controlled using a dual processor Pentium 3 computer. This was located in a room adjacent to the Y maze equipment, and allowed control of the task without interrupting the progress of the marmoset. The computer contained an Apian graphics card that allowed simultaneous video output on four monitors. Three of these outputs were directed to the monitors at the end of each maze arm. The fourth output was used to display task progress on a monitor situated next to

the Y Maze computer. A CCTV monitor was also located next to the maze; this provided an aerial view of the maze and allowed the experimenter to monitor the marmoset's behaviour during the session.

6.2.3 Software

The experimental software was programmed in Visual C++ (Microsoft UK) and interfaced with the national instruments NIDAQ routines. The software was programmed in a real time mode designed to maximise the accuracy of the software timing capabilities. Tasks were specified by providing the software with a tab delimited text file that contained all of the parameters required to run an experimental session. Output was provided in a similar format. Both types of file were created and analysed using MATLAB version 6 (Mathworks UK).

6.2.4 Procedure

A modified version of the two alternative forced choice procedure was used to test marmosets list learning capabilities. The marmosets were trained to locate themselves within the same 'start arm' of the Y Maze upon the presentation of a square wave grating stimulus on the monitor at the end of the start arm. This stimulus was presented at the beginning of every trial and the trial did not commence until the marmoset had responded to it.

Once the marmoset was positioned in the start arm, the square wave grating was removed from the start arm screen and two flower-like stimuli appeared on the two remaining monitors. By moving to the central chamber, the marmoset could view each of these single objects and then make a choice. The two objects corresponded to a

discrimination pair. Upon every presentation of the two objects the same 'positive' object would always be rewarded and the other 'negative' object would never be rewarded.

The marmoset's task was to move into the arm containing the positive object where he would receive a small marshmallow reward via the maze's turntable mechanism. The objects were then removed from the screen and a 2 second delay period commenced followed by the next trial. If the marmoset made an incorrect choice then a longer delay period of 10 seconds commenced.

The side of the maze that contained the positive reward was assigned using a pseudorandom sequence. If the marmoset moved into the side of the maze containing the negative stimulus then the marmoset was not rewarded and a 10 second delay period commenced when all of the mazes screen were blank. This was followed by the next trial.

Marmosets performed 48 trials in this fashion, which constituted a session. When the marmosets failed to achieve this number of trials by timing out prior to the session ending (completion of 48 trials) then all data was discarded for that session. Each session contained four sets of discrimination pairs, therefore each pair was presented on 12 trials. The discrimination pairs were produced so that one of the object pairings contained high contrast colour objects, one contained low contrast colour objects, one pair contained high contrast greyscale (or achromatic) objects and one pair contained low contrast greyscale objects.

The marmosets were provided with the same list until they reached a criterion of above 90% (or 44 correct responses out of 48). Marmosets failed a list if, for the first

list, they produced more than 400 errors over the time course of acquiring the list, or for the second list, they produced more than 200 errors over the time course of acquiring the list. Separate rejection criteria were utilised for the first and second lists, in an attempt to equalise the number of sessions that marmosets performed regardless of whether they passed or failed a list. This was because the marmosets that achieved criterion performed better on list two than list one.

M1	HCP1	LCP2	HGP3	LGP4
M2	HCP2	LCP1	HGP4	LGP3
M3	HCP3	LCP4	HGP2	LGP1
M4	HCP4	LCP3	HGP1	LGP2

Figure 6-2: Example of the counterbalancing regime. Each row refers to the objects that the monkey views. Each of the four object pairs are included within each monkeys list, so that the set of monkeys are tested with all object pairs assigned to all conditions. HC = high contrast colour, LC = low contrast colour, HG = high contrast greyscale, LG = low contrast greyscale. Numbers next to condition refer to the pair number. M1 = marmoset 1, M2 = marmoset 2…..

The objects were designed in such a way that their structural composition was counterbalanced across monkeys. This was achieved using the technique described in Figure 6-2, where each object was produced using high and low contrast colour and greyscale shading. By counterbalancing these objects over all four monkeys, changes in object structure were averaged over the four monkeys.

6.2.5 Stimuli

The objects were structured using the same technique outlined in the general methods. A different methodology was used to shade the constituent elements due the dichromatic nature of the animals used. All objects were shaded using cone excitation values to set the visual properties of the objects (see general methods). As male marmosets have been shown to have cone types that have differing spectral properties, an optimisation algorithm was used to minimise the potential differences between the cone excitation values attributed to the different possible combinations of photoreceptor types. Optimisation was achieved using a Nelder-Mead non linear search method provided by the MATLAB fminsearch methodology.

Colour objects were produced by multiplying the cone excitation values relating to the monitor mid grey background by between 0.55 and 0.95 (high contrast); and 0.05 and 0.045 (low contrast) and using the resultant values to shade object segments. Greyscale objects were produced by the same process; however, the values for each cone type were constrained so that they were equal. Examples of the objects are shown in Figure 6-3.

Figure 6-3: List 2 stimuli. Each of the four object pairs were produced for each of the experimental conditions: HC = high contrast colour, LC = low contrast colour, HG = high contrast greyscale, LG = low contrast greyscale. + refers to rewarded stimuli, - refers to unrewarded stimuli.

6.3 RESULTS

6.3.1 The effect of chromatic subtraction on discrimination ability

The degree to which colour affected the ability of the marmosets to discriminate between objects was examined. This allowed comparison between similar studies in human subjects and macaque monkeys. Specifically the question of whether the removal of chromatic cues had a similar effect in dichromatic subjects as it did in trichromatic subjects was examined.

To compare performance levels for chromatic and achromatic discrimination pairs, measurements were taken of the ability of the marmosets to learn chromatic or achromatic discrimination pairs over a number of experimental sessions. This process was examined by comparing the total number of errors made during the process of learning a list of discrimination pairs. An additional measure was calculated that provided the average percentage of correct trials over sessions when learning chromatic or achromatic discrimination pairs. Both of these measures provided an indication of the marmoset's efficiency in achieving a maximal reward for a discrimination pair.

A third index of performance was calculated that gave the proportion of errors made for chromatic or achromatic objects. This is detailed in Equation 12 and corrected for the overall performance within a list. The value provided a measure of the comparative tendency to make errors within a specific experimental condition. This additional analysis was beneficial, as when the marmosets did not acquire criterion for a list, a value could still be obtained that provided a measure of comparative behaviour for chromatic and achromatic objects.

6.3.2 Overall performance.

Of the four marmosets, two (Chad and Wayne) managed to achieve criterion for one of the two lists. The learning curves for chromatic and achromatic objects (averaged over high contrast and low contrast objects) are provided in Figure 6-4. The other two marmosets (John Luc and John Baptiste) failed both the first and second list. As can be seen from Chad and Wayne's learning curves, failure to reach criterion for a list did not indicate a lack of difference between performance for chromatic and achromatic objects. In both cases the monkeys provided a near perfect level of behaviour for chromatic objects and a near chance level of behaviour for achromatic objects.

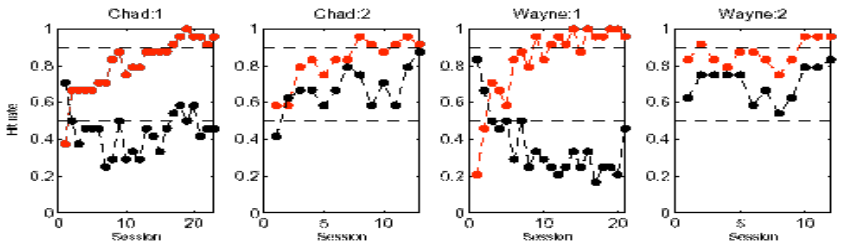

Figure 6-4: Learning curves for Chad and Wayne. The number after the name in the title refers to the list number. Red line provides hit rate for chromatic objects. Black line provides hit rate for achromatic objects.

The average hit rate was obtained by analysing all sessions up to the point where the marmosets passed or failed a list. Data was averaged over sessions to provide a mean value for each list studied by each monkey. This value is sometimes referred to as the mean percentage of correct responses, and is equivalent to 100 times the average hit rate.

When monkeys performed well on an object discrimination, they tended to produce an average hit rate that was nearer the criterion of 0.9, compared with poor

performance being nearer to chance (0.5). This can be seen in Figure 6-4, where the average hit rate for list one chromatic objects was 0.81 for Chad and 0.83 for Wayne and achromatic objects was 0.44 for Chad and 0.36 for Wayne.

Statistical analysis using ANOVA was performed on the mean percentage of correct results for each list. The list number was used as a between subjects factor and the presence of chromaticity was used as a within subjects factor. A main effect of chromaticity was not found ($F_{1,7} = 4.326$, $p = 0.076$, $\delta = 0.435$). When data was examined from lists where the monkeys achieved criterion, a main effect of chromaticity was found ($F_{1,1} = 2717.6$, $p < 0.05$, $\eta^2 = 1$, $\delta = 1$) the monkeys performed significantly better with chromatic objects (colour mean = 0.847, SEM = 0.021) than with achromatic objects (achromatic mean = 0.687, SEM =0.017). This result suggests that despite the lack of an overall difference between the average hit rate for chromatic and achromatic objects, when the marmosets learnt the discrimination pairs within a list, a difference was apparent.

6.3.3 Errors to criterion

The number of errors made for a particular list over all sessions was also examined. Data were examined independently for each list, as the criteria for failing lists were different. A similar pattern of results was observed as with average hit rate, with no significant differences being observed between the number of errors made for chromatic and achromatic objects in the first list ($F_{1,3} = 2.352$ $p = 0.223$, $\delta = 0.193$) or in the second list ($F_{1,3} = 2.968$ $p = 0.183$, $\delta = 0.230$). When analysis was restricted to the lists that the marmosets passed, a significant difference between chromatic and achromatic objects was observed ($F_{1,1} = 2304.0$, $p < 0.05$, $\eta^2 = 1$, $\delta = 1$). The marmosets performed

significantly better with chromatic objects than with achromatic objects (Colour mean = 23 SEM = 4, Greyscale mean = 47 SEM = 4.5).

A measure was also calculated that corrected for differences in the overall performance within each session. The value provided an indication of the tendency of marmosets to produce errors within each of the experimental conditions. For example if the marmoset only produced errors for high contrast achromatic objects, a value of 1 would be obtained for high contrast achromatic objects and values of 0 would be produced for the other types of objects. If the marmoset produced equal numbers of errors across all stimulus conditions then values of 0.25 would be obtained for each of the experimental conditions (see Equation 12 in section 5.3.1).

Statistical analysis was performed by averaging over sessions to produce a mean value for each condition within each list. ANOVA was then performed using the list as a between subjects factor and the stimulus chromaticity and contrast as a within subjects factor. The analysis revealed that the marmosets produced a significantly higher ratio of errors for achromatic objects (mean = 0.309, SEM = 0.025) than chromatic objects (mean = 0.191 SEM = 0.025), ($F_{1,7} = 5.77$, $p<0.05$, $\eta^2 = 0.452$, $\delta = 0.544$). This difference was also apparent when only the lists where the marmosets achieved criterion were analysed ($F_{1,1} = 195.57$, $p<0.05$, $\eta^2 = 0.995$, $\delta = 0.727$: chromatic mean = 0.153 SEM = 0.007, achromatic mean = 0.347 SEM = 0.007).

Reaction time data was also examined. This was in order to establish whether the above differences in performance extended to the time it took the marmosets to indicate a choice within a trial. No differences were observed between achromatic and chromatic

reaction times irrespective of whether or not criterion was reached for a given list (all lists: $F_{1,7} = 0.001$ $p = 0.970$ $\delta = 0.05$; passed lists: $F_{1,1} = 0.428$ $p = 0.631$, $\delta = 0.060$).

Graphical depiction of the effects of colour subtraction are shown in Figure 6-5. A running total of errors produced for chromatic and achromatic objects was calculated and plotted for each session. The cumulative total number of errors made for achromatic and chromatic objects were plotted for each of the two lists performed by the four monkeys. In Figure 6-5, the red line corresponds to the cumulative number of errors made for chromatic objects and the black line corresponds to the cumulative number of errors made or achromatic objects. Charts of this type give a clear indication of the overall level of performance across the time course of the acquisition of a list. They are also less sensitive to the small session based deviations in overall performance, that can be seen in Figure 6-4.

As can be seen from the plots, two of the monkeys (Wayne and Chad) produced curves that showed a clear difference between performance with chromatic and achromatic objects. This was apparent irrespective of whether or not the monkey achieved criterion for a list (both monkeys passed lists two and failed list one). The other two monkeys showed relatively little difference in performance between chromatic and achromatic objects (in list one Jon Luke showed a slight increase in performance for one of the sets of achromatic objects).

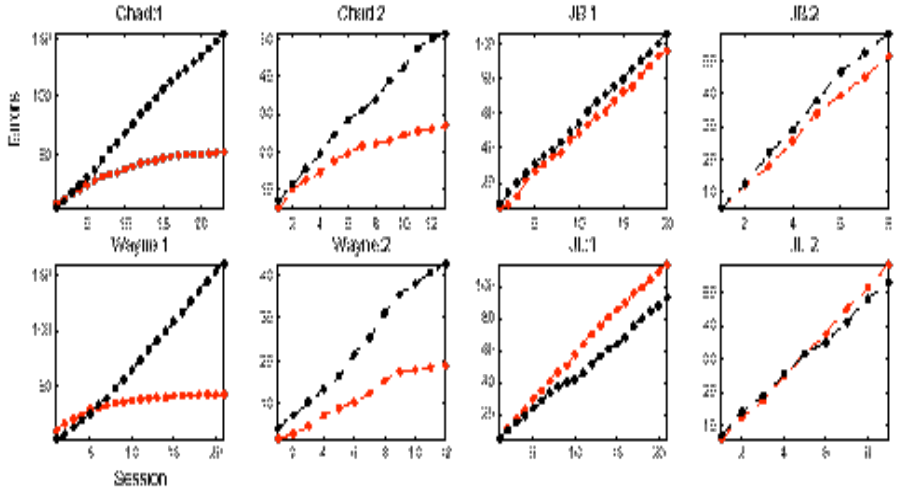

Figure 6-5: Cumulative number of errors for all lists studied by all monkeys. Red line refers to the cumulative number of errors for chromatic objects. Black line refers to the cumulative number of errors for achromatic objects. Number after name in title refers to list number.

In summary, when the monkeys showed an ability to acquire the discrimination pairs present within lists, a difference was observed between chromatic and achromatic objects. This was apparent when comparing the mean hit rates for colour and greyscale objects and the number of errors made during the time course of list learning.

Comparison of a measure of the number of errors made within list sessions that corrected for the overall level of performance within that session also showed a significant difference between performance with chromatic and achromatic objects. This was found irrespective of whether or not the monkey learnt the discrimination pairs within a list. No differences in average reaction times for chromatic and achromatic objects were observed.

These findings are of importance as they show that when marmosets were capable of learning discrimination pairs, the presence of stimulus chromaticity facilitated performance.

6.3.4 The effect of stimulus contrast on discrimination ability

It was also decided to investigate the effect of manipulating the contrast of the object pairs that the marmosets learnt. In previous chapters it was possible to behaviourally equate objects using visual thresholds, thus eliminating the need to consider contrast as a possible experimental factor. Such a technique was difficult with the marmosets as their low level visual mechanisms potentially differed between subject and an exhaustive investigation of these factors was outside the scope of this thesis.

By including two levels of contrast within the experimental design it was possible to assess if the stimulus contrast has an effect on marmoset ability. Based on previous findings it was expected there would be no effect of stimulus contrast and confirmation of this would add further weight to the effects evident by the subtraction of chromatic information.

A similar range of measures were used to assess effects of stimulus contrast as were used to assess effect of stimulus chromaticity. The number of errors made for each session and the fraction of condition specific errors were plotted for colour versus greyscale objects for high and low contrast objects (Figure 6-6).

Each plot represents the complete set of data points taken for each monkey's performance on both lists. Each column represents the data from one of the four monkeys.

The first row represents the comparative fraction of session based errors (as defined by Equation 12 in section 5.3.1) made for high contrast colour and greyscale objects. This is the value between 1 and 0 that indicates how many of the errors made within the session were made within a specific condition (in this case high contrast colour and greyscale objects). The third row represents data from the same sessions with the difference that the points were based upon the number of errors made within a session.

The second row represents the comparative fraction of session errors made for low contrast colour and greyscale objects, the fourth row represents the number of errors made within a session for the same objects. By comparing between the first and second rows and the third and fourth rows it is possible to examine effects of stimulus contrast.

The red points refer to data taken from list one and the green points refer to data taken from list two. Points plotting in the grey segment of the charts show an increased tendency to make errors for greyscale objects compared to colour objects. The number of these points are provided in the top right hand corner of the chart.

The majority of charts show that more errors were produced or the tendency to make errors was greater, for greyscale stimuli compared with colour stimuli. Twelve of the sixteen charts showed a larger number of points plotting in the part of the chart that indicated a deficit in performance for achromatic objects. For all the four other charts, the data originated from monkeys whose overall performance with the lists was poor.

There was a suggestion that this tendency was more pronounced for high contrast objects than low contrast objects. Statistical analysis was therefore performed upon the behavioural data to assess if this tendency was significant.

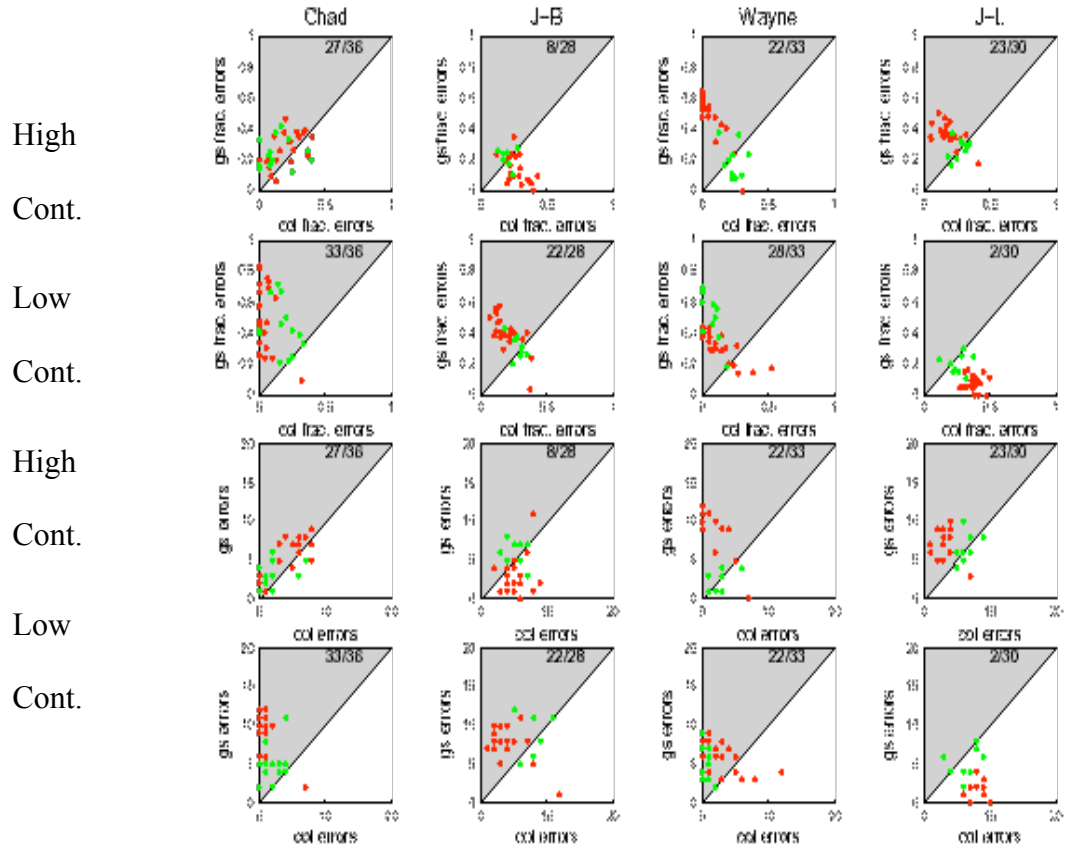

Figure 6-6: Fraction of session based errors and total numbers of errors made in each session for high contrast and low contrast chromatic and achromatic objects. For each plot red points represent performance within a session for list one. Green points represent performance within a session for list two. Columns refer to the data from one monkey. Top and third rows refer to high contrast objects, second and fourth rows refer to low contrast objects. Number in top right hand corner of charts = number of sessions where achromatic errors or fraction of errors were greater than chromatic errors or fraction of errors.

No significant differences were observed between high contrast or low contrast objects irrespective of whether or not the analysis was restricted to lists where the marmosets reached criterion (All lists: $F_{1,7} = 0.809$, $p = 0.398$, $\delta = 0.122$; Passed lists $F_{1,1} = 12.596$, $p = 0.175$, $\delta = 0.219$).

A similar trend was observed when the number of errors for high contrast objects and low contrast objects produced for each list were compared. No significant difference was observed irrespective or whether or not criterion was achieved for a list: (All lists: $F_{1,7} = 0.423$, $p = 0.536$, $\delta = 0.348$; Passed lists $F_{1,1} = 9.878$, $p = 0.196$ $\delta = 0.195$).

In summary no significant differences between high contrast and low contrast objects were observed when measures were employed that factored out the overall level of performance within a session (All lists: $F_{1,7} = 1.914$, $p = 0.209$, $\delta = 0.224$: Passed lists $F_{1,1} = 30.866$ $p = 0.113$, $\delta = 0.337$).

No effect of stimulus contrast was found irrespective of the type of measure used to assess discrimination ability, or whether or not a particular list had been acquired to criterion. This finding is beneficial as it shows that the effects of chromaticity are purely related to the presence of chromatic information, rather than differences in contrast between the various objects used within the experiment.

6.3.5 The effect of object structure on discrimination ability

The objects within the experiment were counterbalanced in such a way that differences in performance caused by changes in object structure within lists were eliminated. Due to the nature of the task it was impossible to counterbalance over successive lists. This was because if objects with the same structural specification but differing chromatic specifications were studied by a single monkey, then the second presentation of the object would be biased by previous experience with that object.

It was therefore of practical and theoretical relevance to examine whether the changes in object structure present between objects of the same chromatic specification across lists, caused deviations in performance. This had implications for the reliability of the study and the comparative importance of structural versus chromatic cues.

The contribution of object structure was examined by comparing marmoset ability with objects of the same chromatic specification but different structural specification. Comparison was performed using the average hit rate across a list, or the average fraction of errors produced for a specific discrimination pair. This value was of relevance as it corrected for the overall number of errors made on a specific list. This was of importance as the criteria for passing lists was different for each of the two lists. It was expected that the higher degree of feature ambiguity present within the objects (the constituent ellipses were similar in appearance) and the nature of the species used would produce no differences in performance across changes in object structure.

Comparison of the average hit rates across the successive lists are shown in Figure 6-7. The bars within each chart refer to the average performance for the same class of stimuli across the four monkeys. The left hand bar and the black crosses relate to performance within the first list and the right hand bar and red circles refer to performance within the second list. As can be seen in the charts, there is very little difference between the average hit rates between the first and second lists for chromatic and achromatic objects of high and low contrast.

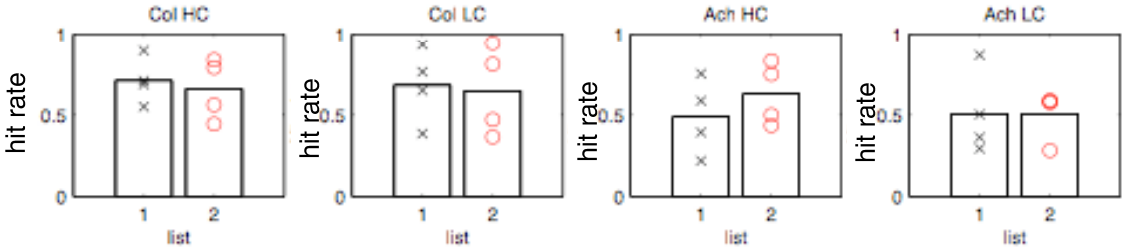

Figure 6-7: Comparison of object based performance within each condition for lists one and two. Black crosses refer to monkey hit rate for a type (eg high contrast chromatic) of object in list one. Red circles refer to list two. Col = Colour objects, Ach = achromatic or greyscale objects. HC = high contrast, LC = low contrast.

This observation is supported by statistical analysis. No effects of list number were found when data were analysed using ANOVA ($F_{1,6} = 0.023$, $p = 0.885$, $\delta = 0.052$). This is reflected in similarities in the mean hit rate for each of the stimulus manipulations within each of the lists: (High contrast colour objects: L1 mean = 0.7114 SEM = 0.07128, L2 mean = 0.6596 SEM = 0.9381; Low contrast colour objects L1 mean = 0.6839 SEM = 0.11554, L2 mean = 0.6488 SEM = 0.13744; High contrast greyscale objects L1 mean = 0.4881 SEM = 0.11635, L2 mean = 0.6296 SEM = 0.09600; Low contrast greyscale objects L1 mean = 0.5072 SEM = 0.12831, L2 mean = 0.5077 SEM = 0.06892).

Similar results were observed when multiple one way ANOVAs were run using the fraction of session based errors from each condition. Each of the four separate ANOVAs produced a non-significant result: (High contrast colour $F_{1,6} = 0.522$ $p = 0.497$; Low contrast colour $F_{1,6} = 0.004$, $p = 0.952$; High contrast greyscale $F_{1,6} = 1.102$ $p = 0.334$; Low contrast greyscale $F_{1,6} = 0.119$ $p = 0.742$).

In summary analysis of the contribution of objects' structure to performance levels revealed no effect of changing structure within chromatic specifications. This finding is of importance as it shows that the effects observed with the manipulations of stimulus chromaticity can only be related to the manipulation of object colour rather than objects structure.

6.4 DISCUSSION

A global deficit in performance was observed for discrimination ability with achromatic objects compared to chromatic objects, when a measure that corrected for session based deviations in performance was used. This was found irrespective of whether the monkey acquired criterion on a particular list. When the data from lists where the monkey reached criterion was analysed, similar deficits were observed using the average hit rate and the number of errors produced in achieving criterion. Effects of extraneous variables were discounted by showing that stimulus contrast or structure has no significant effect on performance.

The finding of a deficit caused by chromatic subtraction further supports the proposal that colour is a stimulus component that is of behavioural relevance. As found within this chapter, the removal of colour impedes the ability to discriminate between objects, and marmosets are capable of discriminating between objects on the basis of chromaticity (Derrington et al., 2002). These findings relate to evolutionary accounts relating to colour playing a functional role for dichromatic species as well as trichromatic species (Anonymous, 1940, Morgan et al., 1992, Williams et al., 1991).

The results are of additional importance as they add further weight to the anatomical and morphological similarities between macaque and marmoset non-human primates. Marmosets and macaques show similarities in the properties of their retina and sub-cortical visual pathway (Troilo et al., 1993, Wilder et al., 1996) and receptive field properties (Kremers and Weiss, 1997, Martin et al., 1997). The commonality of deficit caused by chromatic restriction within each species is encouraging for models of the

visual process that attempt to unite data from both species. It also justifies the use of the marmoset as a model of visual processing akin to old world primates.

One of the major restrictions of the marmoset species that has become apparent from this data, is the time course of learning. Comparative memory performance of marmoset, rat and macaques has already been addressed (Easton et al., 2003). When performing in spatially based tasks marmosets have been shown to perform at similar levels as the rat. One of the major restrictions in the interpretation of the present data was the fact that the marmosets often failed to acquire discrimination pairs.

The finding of a deficit relating to the removal of stimulus colour also converges with findings in human dichromat subjects (Gegenfurtner et al., 1998). The authors conclude that the dichromatic subjects develop tendencies to compensate for their restricted chromatic discrimination abilities. Although a direct comparison between the studies is impossible due to differences in the stimuli and tasks used, it could be suggested that the colour sense in marmosets is present and is vulnerable to chromatic restriction as it is in the trichromatic visual system. Whether this ability in dichromats is enabling the monkeys to segment, recognise or identify the objects is open to future research.

The fact that an effect of colour subtraction has been found in a dichromatic species relates to the evolutionary arguments suggesting that dichromaticity can be advantageous for chromatic discrimination. Studies that show dichromats as capable of discriminating a wide range of ripe from unripe fruit (Sumner and Mollon, 2000) and detecting objects under camouflage (Morgan et al., 1992) are further justification for the chromatic abilities afforded by dichromaticity as being of behavioural relevance.

Dichromaticity fails in situations that require the discrimination between objects that are metamers within a dichromatic space. This is highlighted by the studies that examine foraging abilities with such objects (Caine and Mundy, 2000). In this study a colour space was utilised that eliminated such objects. Although Caine and Mundy's design detracted from the naturalistic underpinnings of the experimental objects it was necessary to ensure that effects of colour subtraction were a product of a limited S cone pathway modulation rather than a lack of trichromatic ability.

The lack of effect caused by changing object structure in this investigation is interesting as it suggests that chromatic cues are of greater importance in the discrimination process than structural cues. A similar finding was observed with the macaque subjects used in Chapter 5 . One (unlikely) possibility is that the marmosets were categorising objects based upon their chromatic content; however, this would have been difficult due to the variability of colours present within the objects. Another possibility is that the type of object used and the high level of feature ambiguity present within the objects made it very difficult to utilise the structural cues present within the objects.

Based upon the above results I intend to investigate the physiological basis of the chromatic deficits outlined within this chapter. The subsequent chapters will investigate the neurological underpinnings of chromatic processing in the marmoset and investigate possible modulations produced by the presence or absence of chromatic information.

Chapter 7 MEASURES OF SINGLE CELL RESPONSE TO CHROMATIC AND ACHROMATIC ELLIPSE STIMULI IN MARMOSET V1

Experimental questions

Do visually responsive neurons in marmoset V1 show selective responses for optimally defined achromatically modulated single ellipse stimuli?

Do visually responsive neurons in marmoset V1 show significant responses for optimally defined single ellipse stimuli containing achromatic and chromatic modulation?

Is cell response caused by the chromatic modulation present within ellipse stimuli selective for a particular colour (for example blue or yellow)?

7.1 INTRODUCTION

This chapter reports experiments in which the response of single cells in marmoset V1 to single ellipse stimuli was recorded. The ellipses were temporally modulated in their luminance (achromatic) or luminance and colour (chromatic) content. The aim of the study was to assess whether cells showed a significant response for these various types of ellipse. It was also of interest to examine whether or not the response caused by the chromatic variations present within a subset of the stimuli, produced a cell response that was selective for a particular colour or combination of colour and luminance (for example they responded selectively to blue-ward modulation or blue-ward modulation accompanied by increases in luminance).

Ellipse stimuli were used, I was interested to explore whether the cells would produce a response to a type of stimulus that was similar to the elements used to construct the objects in Chapter 4 - Chapter 6 . By examining cell response to these types of stimuli it becomes possible to speculate on the possible neural mechanisms that could underpin the advantage that colour affords primate behaviour.

7.1.1 V1 and chromatic responsiveness

The extent to which chromaticity drives cells in V1 is currently debated. Studies in the anesthetised macaque have produced various estimates of the percentage of cells showing strong chromatic tuning. By fitting DKL vectors to the response of cells in V1 Lennie and colleagues found 6 out of 305 neurons showed a strong chromatic response (Lennie et al., 1990). Most cells showed small chromatic effects, however the response in these cells was mostly a product of the achromatic modulation present within the

stimulus. Johnson and colleagues found a similarly small proportion of cells (19 out of 167) that were selectively modulated by purely chromatic stimuli (Johnson et al., 2001).

Studies in awake and behaving macaques have found a larger percentage of cells driven by chromatic cues. The values of cell that have been shown to be significantly modulated by stimuli containing chromatic content has been shown to be as high as 44% for layers 2 and 3 of V1 (Friedman et al., 2003). 65 out of 615 cells surveyed by Conway and colleagues showed red-green selectivity, this was based on the use of high contrast stimuli (Conway et al., 2002).

Based upon the potentially small number of purely chromatically selective cells in V1, recent studies of chromatic function have used stimuli that contain chromatic and achromatic modulation (Derrington et al., 2002). Such a technique is behaviourally and methodologically relevant as very few naturalistic stimuli contain pure chromatic information. This is backed up by studies that use isoluminant stimuli where subjects report objects as having fuzzy edges or that shimmer in appearance (Gregory, 1977). By combining chromatic and achromatic cues, a higher percentage of V1 cells can be driven and the visual stimuli is more suited to investigation of the natural visual process (naturalistic stimuli contain chromatic and achromatic variations). Work has already been conducted using sinusoidal gratings and stimuli of this type. In order to investigate the neural processing of the objects used in Chapter 4 - Chapter 6 , I presented ellipse stimuli containing achromatic and chromatic variations to V1 cells.

As cells in V1 have been found to respond to stimuli containing chromatic and achromatic modulation, questions have emerged concerning the degree of cortical segregation between these stimulus attributes. Current views of the functional properties

of V1 suggest that luminance and chromaticity modulations are represented simultaneously. Signals are conveyed simultaneously by single cells rather than being represented explicitly by separate populations of cells. This 'double-duty' hypothesis suggests that the same cell is capable of representing achromatic and chromatic signals (Lennie, 1998). Such a process could arise from the lateral connectivity within a cortical area or possibly feed-forward and feedback connections between anatomical areas.

Other theories suggest that the chromatic and achromatic signals are segregated and processed by distinct cortical areas (Zeki, 1983c, Zeki, 1983a, Zeki, 1983b). Although a range of experimental studies have supported this hypothesis, recent work has shown that cortical areas represent multiple stimulus attributes, and the same attribute is represented in multiple cortical areas (Tootell et al., 2003). The balance of evidence emerging from a variety of techniques suggests that the original suggestions of Zeki regarding the role of V4 in chromatic processing are limited (Walsh et al., 1993, Merigan and Pham, 1998, Merigan, 2000)

7.1.2 V1 and chromatic selectivity

Further questions emerge concerning the way in which cells in V1 respond to chromatic variations. Some studies have concluded that V1 contains cells that with a few exceptions respond to chromatic modulation as would be predicted from the linear model (Lennie et al., 1990). Responses of this nature also typify the way in which LGN cells respond (Derrington et al., 1984). A prevalence of colour opponent cells in V1 has been proposed by a modelling study that incorporated data from fMRI studies and single unit studies (Schluppeck and Engel, 2002). Others studies have found that the cells show a unipolar (or rectified) chromatically selective response (selective for a particular type

of colour e.g. blue or yellow), (Wachtler and Sejnowski, 2003). Psychophysical work has also converged with the theory of chromatic detection mechanisms being based upon unipolar / rectified mechanisms (Sankeralli and Mullen, 2000).

There are several behavioural reasons for doubting the fact that the chromatic opponency present in the retina and LGN remains at cortical levels. Subjects report that psychophysically isolated cone mechanisms do not appear uniquely red, green, blue or yellow (De Valois and De Valois, 1993). There must therefore be some from of combination or transformation of opponent units to form the colour sensation. Secondly, thalamic neurons are widely accepted as being capable of rectifying response. The conversion of bipolar to unipolar response could therefore occur over a single neuron. This process could provide V1 with a functionally important increased degree of chromatic selectivity. Work is therefore required to clarify whether the population of cells in V1 respond to chromatic information in a bipolar, unipolar or bipolar and unipolar fashion. For example do V1 neurons respond in a way that suggests they only signal red-ward chromatic modulation or do they continue to act in a antagonistic red-green manner.

In the experiments detailed in this chapter I recorded the response of cells in marmoset V1 to single ellipse stimuli that were modulated temporally using luminance variations or luminance and chromatic variations. As no studies have assessed the ability of V1 cells to respond to ellipse stimuli, the effectiveness of the stimulus in driving V1 cells was also examined. It was expected that the ellipses would be effective in driving visual cells and that the distribution of width and length values would be similar to values found by studies that have used bars. I manipulated the ellipses in terms of their

width, length and orientation in order to establish a maximum response and then compared these stimulus characteristics to other studies.

Having established a subset of cells that responded to achromatic single ellipse stimuli further work was performed in order to examine whether a similar number of cells (taken from the same population) were significantly modulated by the ellipses that contained chromatic and achromatic modulations. It was expected that a slightly smaller number of cells would be modulated by ellipses containing both chromatic and achromatic variations than were modulated by ellipses containing just achromatic modulation.

If was of further theoretical relevance to determine whether or not cells responded to the chromatic variations present within the stimulus in a selective or unselective way. An understanding of the degree of chromatic selectivity that cells exhibited would also help inform theories of V1 function. It was expected that cells would fire in a unipolar and a bipolar fashion, thus exhibiting a range of selectivity for chromatic content.

7.2 METHODS

7.2.1 Subjects

Four common marmosets were used in the study. Details on the surgery, histology anaesthesia and recording routines are provided in the general methods. Neuronal recordings were performed using an anesthetised setup.

7.2.2 Procedure

In order to generate the stimulus set used in this experiment it was necessary to define the properties of an ellipse that produced maximal response when presented in the centre of a cells receptive field. Cells were characterised using sinusoidal gratings. The position, size, width, length, orientation, spatial frequency and temporal frequency of the gratings could be altered and the effect this had on cell firing was observed and recorded. Several pre-tests were run to determine a cells' tuning curves for the orientation, spatial frequency and temporal frequency preference. Example data from these tests is shown in Figure 7-1. Further tests were run to establish the size and profile of a cells receptive field. When an optimal grating had been established a further test was utilised to ensure that the grating was placed centrally within the cells receptive field.

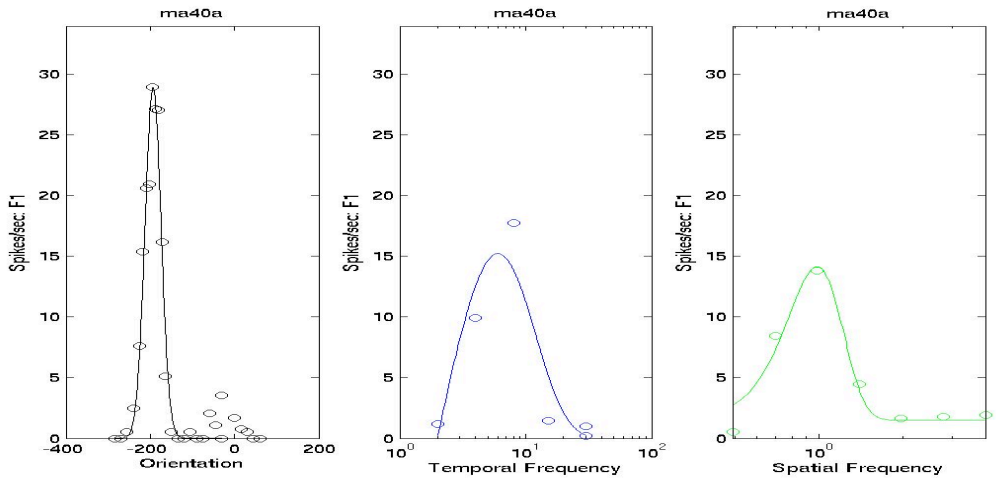

Figure 7-1: Example of cell tuning to sinusoidal gratings of variable orientation, temporal frequency and spatial frequency.

The test that checked that gratings were located centrally consisted of an annulus stimulus. A circular grating was generated at the optimal grating position, size, spatial frequency and orientation. The interior dimensions of the annulus (the hole in the middle of the circular grating), was set to the size and position of the cells' optimal grating. The exterior part of the annulus (sinusoidal in nature) extended from the external boundary of the optimal grating to twice the radius of the optimal grating. The response to this grating was recorded over several presentations and then averaged. A measure of the cells' spontaneous rate was also taken. By comparing responses to the two stimuli it was possible to determine whether the optimal grating was positioned correctly, as in this case the external part of the annulus caused no deviation from the spontaneous firing rate.

Having defined the sinusoidal grating that optimally modulated the cell it was necessary to obtain the dimensions of the ellipse that produced the maximal response when rendered at the same orientation as the optimal grating centrally within a cells

receptive field. Two tests were utilised, these rendered ellipses of varying width and length positioned centrally within the cells' receptive field.

Stimuli were modulated temporally as well as spatially. Rendered ellipses alternated between the maximum and minimum achievable monitor luminance output. This occurred at a rate found to produce a maximal cell response. Ellipse luminance was varied sinusoidally over time. The screen background was set to the monitors mid grey level. A complete stimulus cycle therefore consisted of the stimuli being presented at full intensity and then the stimulus luminance decreased and then increased through the background mid grey level

Ellipses were rendered at 8 or 9 width and length dimensions, set to between 0.08 and 8 degrees of visual angle in size. Optimal ellipse width was obtained first and then used as the width parameter for the ellipses of varying length. For both tests, each dimension was randomly presented 4 times, and cell response was averaged over presentations. A measure of spontaneous activity was also taken.

7.2.3 Stimuli

In order to address the experimental questions outlined at the beginning of this chapter ellipses were required that contained either achromatic modulation or chromatic and achromatic modulation. For all tests that involved presenting ellipses, the DKL colour space was used to specify the colour and luminance of the presented ellipses (see general methods for information relating to the DKL colour space). The DKL space was chosen to allow comparison with the behavioural results reported in Chapter 3 to Chapter 6 .

All ellipses containing chromatic modulation used in the following two chapters were directed along the constant LM axis of the space (the axis spanning 90 to 270 degrees). All ellipses containing chromatic modulation also contained luminance modulation, such that the elevation of the DKL vector spanned from 45 degrees to minus 45 degrees (see Figure 7-4). All achromatic ellipses were based upon a DKL vector of 90 degrees elevation.

The chromatic modulation was defined so that it followed the time course of the luminance modulation. There were three types of stimulus modulation.

1) Achromatic (luminance defined), Sinusoidally modulated over a time course defined by the cells optimal temporal frequency.
2) Chromatic and achromatic (defined by luminance variations and chromatic variations), Yellow-ward chromatic modulation accompanied positive luminance modulation, blue-ward chromatic modulation accompanied negative luminance modulation.
3) Chromatic and achromatic (defined by luminance variations and chromatic variations), Blue-ward chromatic modulation accompanied positive luminance modulation, Yellow-ward chromatic modulation accompanied negative luminance modulation.

All cells were classified into simple cells and complex cells using the criteria outlined in the general methods. Cells were rejected from the analyses if their average firing rate was less than five spikes per second. The recorded waveform was analysed using the methodology outlined in the general methods. For the width and length tests

the data points were fitted using a difference of Gaussians curve (outlined in the general methods). Bonferonii corrected t-tests were utilised to investigate whether cells produced a significant response compared with the spontaneous firing rate.

7.3 RESULTS

The aim of the following two chapters was to establish the way in which V1 cells responded to the elements used to construct the objects used in Chapter 4 - Chapter 6 . Cell response was recorded for single ellipse stimuli that were modulated achromatically or were modulated both chromatically and achromatically.

It was important to ensure that cells in V1 showed a significant response when driven by these types of stimulus, as the majority of studies that examine cell function in V1 use sinusoidal gratings. It was of additional interest to examine whether the response to the single ellipse stimuli was selective for the various properties of the stimuli. These included the width and length of the stimulus, whether or not chromatic variations were present in the stimulus and whether response was dependent upon the type of chromaticity present within the stimulus.

7.3.1 Measures of the response of V1 cells to achromatically modulated single ellipse stimuli.

In order to understand whether or not cells in marmoset V1 responded to achromatic ellipse stimuli, and whether this was selective for the dimensions of the ellipse, cell response was measured for single ellipses of varying widths and lengths. Based upon previous studies that have used sinusoidal gratings, it was expected that the majority of cells would respond in a selective way to a single ellipse of specific dimensions. By testing cell response to various achromatic ellipses of differing widths and lengths, it was possible to obtain a profile of the cell response characteristics to the spatial properties of the ellipse.

Figure 7-2 shows an example of cell response for a complex cell in V1. A difference of Gaussian curve was fitted to the obtained data points using the techniques outlined in the general methods (Chapter 2). The obtained functions approximated the data well, the fraction of variance explained (FVE) value was 0.92 for the width data points and 0.94 for the length data points. The cell shows a reliable peak response of between 18 and 20 spikes per second. The curves fitted to the data points relating to changes in ellipse length and width are typical of the type of response that would be expected from various models of the receptive field properties of V1 cells. The cell appears to be end-stopped, as increases in length beyond 1 degree produce a diminishing response.

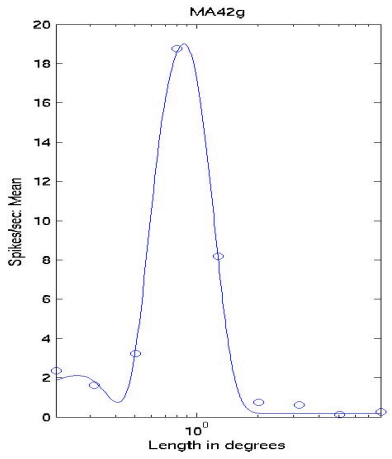

Figure 7-2: Example tuning curve for cell response to ellipses of variable lengths. Fitted line = best fit difference of Gaussian curve.

A similar technique was used to fit difference of Gaussian curves to the width and length response curves from all cells that were tested. The fitted curves explained more than 90% of the variance in the data for all of the cells used (if the fitted curve explained less than 90% of the data then the cell was rejected – five cells were rejected

due to not meeting this criterion). Overall a mean FVE value of 0.95 was achieved for the data set. The fitted curves were then used to obtain a value for the optimal ellipse widths and lengths. The range of obtained values was between 0.12 degrees and 7.34 degrees of visual angle (mean 0.97 degrees standard deviation = 1.64, skew = 3.29, kurtosis = 10.796, Komolgorov-Smirnov$_{25}$ = 3.50 p = 0.000) for the widths and between 0.22 and 8.01 (mean 4.81 standard deviation = 2.74, skew = -0.338, kurtosis = -1.466, Komolgorov-Smirnov$_{25}$ = 0.182, p = 0.32) for the lengths. The distribution of the optimal width and length values is shown in Figure 7-3. In this figure, the grey shapes in the chart background represent an example of the type of ellipse that data points refer to. The plus symbols refer to data from simple cells and the cross symbols refer to the data from complex cells.

Aspect ratio values were calculated for the optimal width and length values for each cell. The aspect ratio was calculated by dividing the optimal width by the optimal length. The distribution showed a large degree of positive skew (skew = 1.829, kurtosis = 2.586 Komolgorov-Smirnov$_{25}$ 25 = 0.295, p =0.000). The minimum aspect ratio was 0.02, the maximum was 0.7. The mean aspect ratio value (0.5) used to construct the objects in Chapter 4 - Chapter 6 fell within this range.

A Bonferonii corrected paired samples t-test was used to assess statistical significance between the spontaneous firing rate and the response to the optimally defined ellipse. In total 25 out of 28 of the included cells were found to be significantly more responsive for the ellipse stimuli compared with their spontaneous rate ($P < 0.05$ – Bonferonii corrected). These cells are depicted by red symbols in Figure 7-3. Of the

significant cells 15 were simple cells and 10 were complex (see methods for a definition of simple and complex cells).

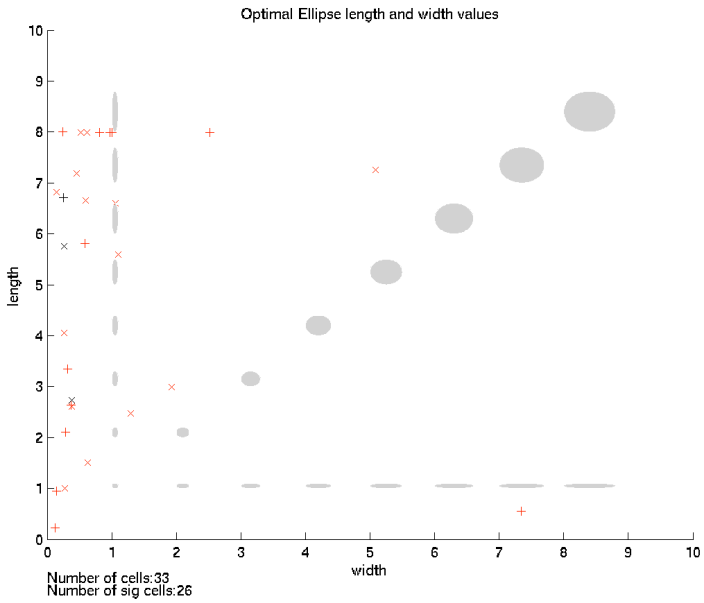

Figure 7-3: Chart of optimal ellipse length and width parameters from the fitting routine used for all cells. Plus points = simple cells, Cross points = complex cells, Red points = significantly modulated cell. Grey ellipses / circles = example of stimulus.

As can be seen in Figure 7-3 all apart from 2 cells showed an optimal response to larger ellipse lengths than widths. This fits in with the classical view of the nature of RF properties in V1 where cells are found to respond to elongated strips of light (Hubel and Wiesel, 1962). To the best of my knowledge no other studies have examined the spatial characteristics of optimally defined ellipses in marmoset V1 (this is possibly because they are very similar to the more intensively studied line stimuli) . However in a study using bars of optimum length and width and a subset of marmoset V1 cells that responded to first and second order stimuli, Bourne and colleagues produced estimates of the distribution of length values for optimum bar stimuli. The authors found a

distribution of optimal lengths of between 1.7 and 13 degrees and optimal width values of between 1 and 10 degrees (Bourne et al., 2004, Bourne et al., 2002). In the present study much smaller values of optimal ellipse length were found and no cells responded optimally to ellipses of more than 7 degrees. This discrepancy could be due to the sampling restrictions applied by the authors in order to study form-cue invariant neurons.

In summary it was possible to drive the majority of V1 cells using single ellipse stimuli corresponding to the elements used within the objects detailed in Chapter 4 - Chapter 6 . Cells showed optimal width and length tuning, in line with previous studies of marmoset V1, with the exception that in this study optimal responses were found for ellipses of lengths below two degrees. Cell response was found to be significant in a large proportion of the cells (25 out of 33) and cells were generally found to respond to ellipses where the length was greater than the width.

7.3.2 Measures of the response of V1 cells to chromatically and achromatically modulated single ellipse stimuli.

Having documented a population of V1 cells that showed a significant response to ellipse stimuli, I wanted to investigate whether a similar number of cells showed a significant response when chromatic and achromatic modulation was present within the stimulus. I was interested in whether or not a similar number of cells showed a significant response for achromatically and chromatically modulated ellipses as they did for achromatically modulated ellipses. Two types of ellipses were compared, those that contained only achromatic modulation, those that contained achromatic and chromatic modulation. In order to fully classify whether or not cells were responding to ellipses

containing chromatic information, two types of chromatic and achromatically modulated ellipses were used.

In one type of ellipse, increases in luminance accompanied changes in chromaticity towards the yellow end of the DKL constant LM axis, and decreases in luminance accompanied changes in chromaticity towards the blue end of the DKL constant LM axis. In the other type of ellipse increases in luminance accompanied changes in chromaticity towards the blue end of the DKL constant LM axis, and decreases in luminance accompanied changes in chromaticity towards the yellow end of the DKL constant LM axis. It was necessary to use these two types of ellipse, as if cells were selective for a combination of specific luminance and chromatic modulation, then a complete survey would require specific shifts in chromaticity to accompany both increases and decreases in luminance.

Also of interest was the comparative phase of the extracted Fourier response for achromatically modulated ellipses and chromatically and achromatically modulated ellipses. A Fourier response is a measure of the degree to which a cell shows modulation at a specific frequency. If (for example) a cell showed a response that was similar to a 2Hz sinusoidal wave then the extracted Fourier component at 2Hz would be much larger in amplitude than the extracted Fourier component at 3Hz.

The phase of a Fourier response is a measure of the offset that the modulation shows compared with (for example) the modulation of the stimulus. If a cell showed a peak in response, when the stimulus was showing a dip in intensity then the offset would be equivalent to half the cycle of modulation. The stimulus would therefore be leading the cell by a phase of 180 degrees. By comparing the phase of the different cell response

for the same or similar stimuli it is possible to compare the way in which cells respond. Different cells may (for example) be responding to the same stimulus with a different latency.

I was interested in whether or not the phase of response for a given cell was different for achromatically and achromatically and chromatically modulated stimuli. If a difference was apparent then it would suggest that the cells were responding in a different way for the chromatic variations in the ellipse than the achromatic variations in the ellipse.

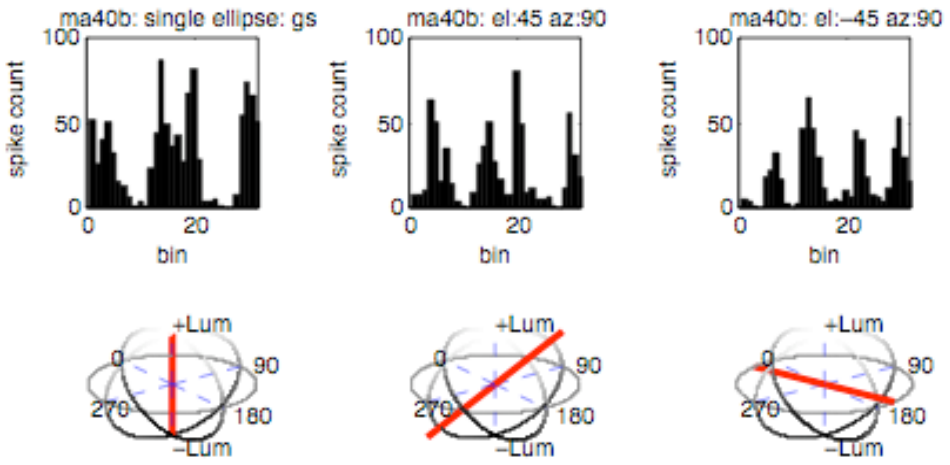

Figure 7-4: Top row = PSTHs for two stimulus cycles depicting the response of a complex cell to the three types of ellipse. Left plot = achromatically modulated ellipse. Middle plot = achromatically and chromatically modulated ellipse (yellow shifts accompany increases in luminance). Right plot = achromatically and chromatically modulated ellipse (blue shifts accompany increases in luminance). Bottom row = Axis of modulation in DKL space.

Figure 7-4 shows peri-stimulus time histograms (PSTH's) for a complex cell in marmoset V1. The plot on the left hand side of the figure displays example response for

a single optimally defined achromatic ellipse. The stimulus contained no chromatic modulation and produced an average cell firing rate of 30.93 spikes per second. The middle and right hand plots show that when the same cell is tested using the same ellipse modulated so that it contained chromatic variations as well as achromatic variations, a reliable response is still observed.

The cell produced an average firing rate of 20.87 spikes per second for an ellipse modulated along the constant s cone axis, with positive luminance modulation at the 90 degree (yellow-ward) end of the axis. When the same axis of chromatic modulation was used, but with positive luminance modulation at the 270 degree (blue-ward) end of the axis then a similar average firing rate of 18.45 spikes per second was recorded.

It was unlikely that the cells response to chromatic and achromatic ellipses was purely a component of the achromatic modulation within the ellipse as for the same cell a small but significant response was observed for purely chromatic optimally defined sinusoidal gratings (spontaneous firing subtracted, $t_5 = 11.1046$, $p < 0.05$, mean count = 5.911).

Having established that V1 cells exhibited a response to ellipses containing achromatic and chromatic modulation a population analysis was conducted on the 33 cells detailed in the previous section 7.3.1 in order to show how many produced a significant response for single ellipse stimuli containing achromatic and chromatic modulation of the type detailed in the methods.

Of the 27 cells, 12 were rejected from the analysis as the average spike count was below five spikes/sec. Of the remaining 15 cells a single sample Bonferonii corrected t-test revealed that 9 cells showed a significant response to the single ellipse

stimuli that were chromatically and achromatically modulated. The small number of cells of this type was possibly due to the fact that V1 neurons convey multiple stimulus attributes, many of which we did not test for. Of these cells 4 were defined as simple and 5 defined as complex (see general methods). For the 9 significantly modulated cells an additional analysis was performed in order to compare the phase values of the optimal frequency component obtained for the cell response for achromatic ellipses and ellipses containing chromatic and achromatic modulation.

Having established a subset of cells that responded reliably to the chromatic and achromatically modulated single ellipse stimuli, further analysis was performed in order to examine the relationship between the time course of cell response and the time course of the stimulus. In order to make this comparison, only the ellipses that contained luminance variations that were in phase were examined.

For a given cell, if the PSTH's for achromatic ellipses and ellipses containing chromatic and achromatic information took a similar form (despite differences in the average firing rate) then it would suggest that similar mechanisms were producing a response for chromatic response and achromatic response. In this case the peaks of the modulation observed within each PSTH would overlap and the phase of the extracted Fourier component (at the optimal temporal frequency) would be the same. The cell would be responding in exactly the same way (all be it at a lower or higher rate) for both types of ellipses.

If a different type of response was produced for achromatic ellipses and ellipses containing chromatic and achromatic modulation then the PSTH's would take differing forms and the phase of the extracted Fourier component would be different. This would

suggest that by adding chromatic information, a change in the time course of response was present rather than a change in magnitude of response.

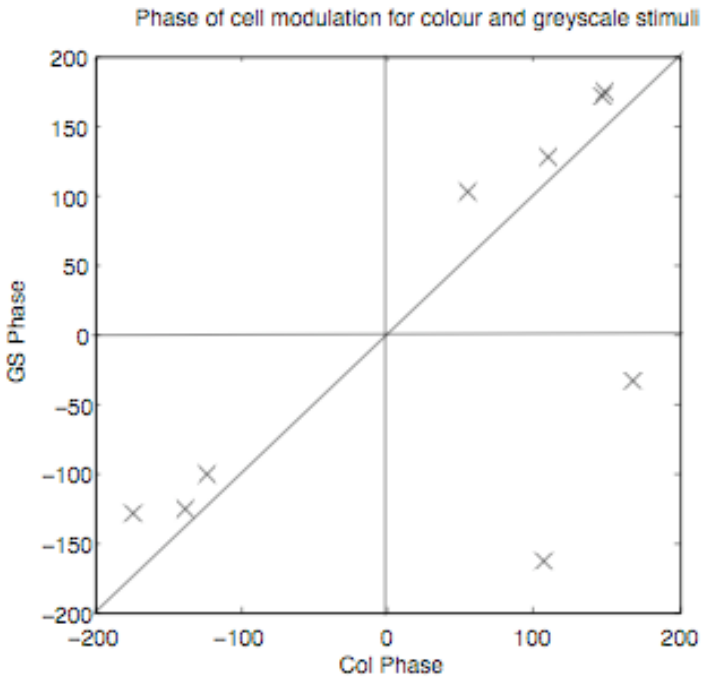

Figure 7-5: Comparative phase of the extracted Fourier component for the same cell modulated by achromatic (GS phase) ellipses and achromatic and chromatic (Col phase) ellipses.

Figure 7-5 shows the phase of the extracted Fourier component for the subset of cells described in the previous section 7.3.1. The phase was calculated for simple and complex cells, as the complex cells still provided PSTH's that showed a degree of modulation in response in line with the temporal frequency. The figure shows that the majority of cells showed no difference in the phase of response for the ellipses containing achromatic modulation and the ellipses containing chromatic and achromatic modulation. This is apparent by the fact that most points lie on the line connecting the points where the phase for the two types of stimuli were equivalent.

Only 2 cells did not fit this pattern and therefore showed differential modulation for ellipses containing chromatic and achromatic information than for ellipses containing only chromatic information. For these cells the addition of chromatic content was causing the cell to fire in a different way than it did for achromatic stimuli. In conclusion far fewer of the surveyed cells showed a reliable response to ellipses containing chromatic and achromatic information than did for ellipses containing purely achromatic information. Where cells did show a reliable response for the class of optimally defined single ellipse stimuli containing both luminance and chromatic modulation, the phase of response was generally the same as that for the same ellipses containing only luminance modulation. A very small subset of the cells (2 cells) showed differences in the phase of their response for the different classes of ellipse. Further study is required in order to examine the role that these cells play in the process of visual perception.

7.3.3 Measures of chromatic selectivity for cell response to single ellipse stimuli

Two types of ellipses were used that contained chromatic and achromatic modulation. In the first condition blue-ward modulation accompanied decreases in luminance and yellow-ward modulation accompanied increase in luminance. In the second conditions, blue-ward modulation accompanied increases in luminance and yellow-ward modulation accompanied decreases in luminance. Example PSTHs are shown in Figure 7-6. By examining the way in which cells were modulated by the stimuli it was possible to deduce whether or not the cells showed a degree of selectivity for the chromatic signals present within the stimulus. I wanted to assess whether the contribution of chromatic modulation on cell response was dependent upon whether the

type of chromaticity modulating the cell was accompanied by a luminance increment or decrement.

Of the 9 cells that were found to be significantly modulated by chromatic modulation accompanying luminance modulation, 4 showed a significant response unique to one of the above conditions (Bonferonii corrected t-tests). Of these cells one was significantly modulated when yellow chromatic modulation accompanied increases in luminance and three were significantly modulated when blue chromatic modulation accompanied increase in luminance. This is shown by Figure 7-6, that depicts a simple cell in V1. For the achromatic ellipses, the cell only responded to negative deviations in luminance. For the chromatic and achromatic ellipses, the cell responds well to one type of chromaticity (blue-ward) accompanied by decreases in luminance. For the second condition, where the same colour is accompanied by an increase in luminance the cell responds poorly. The cell is therefore showing a degree of chromatic selectivity along with luminance selectivity. The cell produced a mean Fourier amplitude of 9.47 for the condition where blue-ward chromatic shifts were accompanied by decreases in luminance and 4.53 for the condition where blue-ward chromatic shifts were accompanied by increases in luminance.

This is also apparent in the phase of the extracted Fourier component, the phase of the left hand histogram being 148 degrees and the phase of the right hand histogram being -5 degrees. The fact that the phase of the right hand histogram lead the left hand histogram by 152 degrees further highlights the chromatic selectivity of the cell.

Cells therefore showed a tendency to respond in both a selective and unselective fashion for the different types of chromaticity used within the stimulus. In some cells

this was coupled with selectivity for the direction of the luminance deviation (from the mid point). The small numbers of selective cells found show that cells of this nature are rare and further investigation would be of benefit.

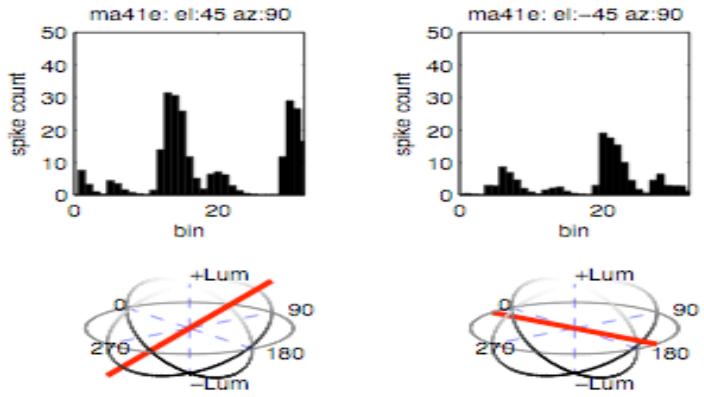

Figure 7-6: Top row = PSTHs for two stimulus cycles depicting the response of a complex cell to two types of chromatically modulated ellipse. Left plot = achromatically and chromatically modulated ellipse (yellow shifts accompany increases in luminance). Right plot = achromatically and chromatically modulated ellipse (blue shifts accompany increases in luminance). Bottom row = Axis of modulation in DKL space.

7.4 DISCUSSION

In conclusion the vast majority of cells (25 our of 33) showed a significant modulation for the ellipses containing achromatic modulation. The cells showed a degree of preference for ellipses of specific widths and lengths (as would be expected from previous studies using sinusoidal gratings). Far fewer cells showed significant modulation for the ellipses containing chromatic and achromatic variations (12 out of 33). Of these cells one was significantly modulated when the yellow-ward variations were accompanied by increases in luminance but not when variations were accompanied by decreases in luminance and 3 were significantly modulated when the yellow-ward variations were accompanied by decreases in luminance but not when accompanied by increases in luminance.

Comparison of the phase of the extracted Fourier component for the various types of ellipse showed that the ellipses that contained both chromatic and achromatic variations responded in a different way to the achromatically modulated ellipses. This was observed in 2 cells and was caused by the chromatic component of the ellipses that contained both chromatic and achromatic modulation. Further comparison of the f1 and f2 Fourier amplitudes showed that cells responded to the chromatic variations in a selective and an unselective way. Cells therefore showed a tendency to respond to blue and not yellow and to respond to yellow and not blue.

Due to the need to obtain reliable measures of cell response it was necessary to modulate the chromatic and achromatic content of the ellipses. In a naturalistic setting variations in luminance and chromaticity within an object are in no way equivalent to the time course of modulation used in this experiment (changes occur over a period of

hours rather than seconds). This is an obvious restriction in the experimental methodology, despite this, it is argued that the need to drive cells would have made reliable measurements of the response to un-modulated stimuli impossible.

The fact that the cells showed a tendency to show selectivity for specific widths and lengths of ellipses, suggests that the cells shown a degree of spatial antagonism. Apart from the few non-end-stopped cells that were found, all cells showed a specific tuning for a particular length and width. The findings would suggest that the cells showed a degree of inhibition for extensions along the width and length axes past the optimal values ellipse. The range of optimal stimulus widths and lengths found is similar to those found in studies that have used bar stimuli to assess the spatial characteristics of cells in V1 using similar methodologies in the same species (Bourne et al., 2004, Bourne et al., 2002).

Studies in cats and macaques also find a degree of spatial antagonism typical of the 'Gabour patch' or 'difference of Gaussian' model of V1 receptive fields (Sceniak et al., 2001, DeAngelis et al., 1995, Jones and Palmer, 1987a, Deangelis et al., 1993, Shapley and Reid, 1991). A route for further investigation is to find out how the ellipse stimuli interact with these models, when ellipses are placed in the extra classical receptive field surround (see next chapter).

A large body of work has been conducted about the comparative responsiveness of V1 cells to purely chromatic and purely achromatic gratings. Studies have found that most cells respond optimally to gratings containing either purely achromatic modulation or a combination of chromatic and achromatic modulation. In the case of this study, the chromatic conditions utilised ellipses with chromatic and achromatic modulation.

Therefore the relatively large proportion (aprox. 35%) of cells found to be significantly modulated by the ellipses containing chromatic and achromatic modulation (compared with the values found for purely chromatic stimuli – around 2%- 11% (Lennie et al., 1990, Johnson et al., 2001)) can be accounted for by the presence of achromatic variations. There was a possibility that the high number of cells significantly modulated in the chromatic conditions were only being modulated by the luminance component of the stimuli. This possibility can be excluded for the majority of the responsive cells by the fact that the cells showed a significant response to equiluminant stimuli or a phase difference between the response to achromatic stimuli and stimuli containing chromatic and achromatic modulation.

The fact that cells were found that were significantly modulated when a chromatic change was accompanied by an increase in luminance but were not significantly modulated when a chromatic change was accompanied by a decrease in luminance is also important. Psychophysical studies debate the independence of the chromatic and achromatic processes (Mullen and Losada, 1994, Gowdy et al., 1999). Based upon these findings (luminance direction having an effect upon the chromatic responsiveness of a cell) it seems probable that there is a degree of interaction between chromatic and luminance signals. This converges upon the findings of Derrington and colleagues, where shifts in background chromaticity had an effect upon the response to an achromatic grating (Derrington et al., 2002).

A subset of neurons were found that showed selective modulation for one type of colour (e.g. blue) and not the equivalent opponent colour (yellow). This is the type of response that would be produced from the unipolar mechanisms suggested by the

psychophysical literature (Sankeralli and Mullen, 2000, Krauskopf et al., 1982). Cells of this nature have already been found by studies using an awake behaving methodology (Wachtler and Sejnowski, 2003). This is an important result, as the prevalence of these types of cell is currently debated.

Large scale models of cortical function have proposed that the increased feature selectivity observed along the visual pathway is a product of two general processes (Riesenhuber and Poggio, 2000). Cortical invariance relates to the fact that neurons respond to an image, irrespective of various transformations, such as size orientation or position. Specificity relates to the ability to respond in a selective way for a specific stimulus and not for others. The fact that chromatically selective and non-selective cells are present in V1 could relate to the fact that both selective and non-selective neurons could be required to meet the requirements for these competing needs.

Further work is required in order to examine several issues relating to V1 cell selectivity that have not been addressed in this chapter. Firstly does the extension of the ellipse stimulus (by an additional ellipse) modulate cell response to a greater or lesser extent to the responses found in this chapter. Such a stimulus (originally defined as hypercomplex (Hubel and Wiesel, 1962) would suggest that cells in V1 are capable of showing a differential responding to combinations of ellipses. Secondly does chromatic selectivity remain when stimuli are extended outside the classical repceptive field.

Chapter 8 MEASURES OF SINGLE CELL RESPONSE FOR TWO ELLIPSE STIMULI RECORDED IN MARMOSET V1

Experimental questions

Is cell response to a single optimally defined achromatic ellipse stimulus modulated by the addition of a similar achromatic flanking ellipse stimulus?

Is cell response to a single optimally defined chromatic and achromatically defined ellipse stimulus modulated by the addition of a similar flanking ellipse stimulus?

Is modulation in response caused by the addition of chromatic flanking ellipses affected by the chromatic specification of the constituent ellipses?

8.1 INTRODUCTION

In this chapter the response of single cells in V1 were measured using the ellipse stimuli shown in Figure 8-1. A single optimally defined ellipse was placed centrally within the cells receptive field and a second similar flanking ellipse was placed in the outer part of the receptive field. The orientation of the flanking ellipse was varied in order to assess the symmetry of the classical receptive field.

I wanted to find out if the cell response was significantly modulated by placing the additional ellipse stimulus outside of the cells classical receptive field and whether or not this was specific to the orientation of the ellipse placed in this area (the flanking ellipse). I also wanted to examine if the chromatic content of the ellipse had an effect on the degree to which cell response was modulated by the addition of a second ellipse and whether this modulation was specific to a certain direction in colour space.

Various theoretical accounts have been proposed relating to the way in which V1 cells respond to modulations in luminance over the spatial dimensions of a stimulus. A range of studies have shown that cells in V1 have receptive fields that respond in a way similar to linear spatial-temporal filters. These have been modelled using Difference of Gaussian (DOG) (Deangelis et al., 1994) or Laplacian of Gaussian (LOG) functions (Marr and Hildreth, 1980).

These functions have been used to accurately fit a wide range of empirical data relating to the spatial selectivity of the response of V1 cells (Hawken and Parker, 1987, Jones and Palmer, 1987a, Field and Tolhurst, 1986). Operators of this type have also been shown to be efficient in producing a sparse representation of the visual scene.

The type of basis function (filter) produced from the statistical analysis of natural scenes has been shown to resemble models of the receptive field profile derived from empirical study. (Simoncelli and Olshausen, 2001). Models of this nature aim to optimise the efficiency of statistical models in coding for luminance variations in natural scenes.

Although the vast majority of studies converge upon the above findings, in one study a small number of cells were discovered that showed receptive field properties with spatial characteristics that were atypical (asymmetric) in nature (Conway et al., 2002). This has allowed researchers to consider the possibility that V1 receptive fields may not exclusively comprise of spatial filters that have a linear profile. Modelling work has shown that the necessary cortical apparatus to detect curved lines could be derived from the differencing of end stopped neurons (Dobbins et al., 1989). Such units would be of potential benefit in the efficient representation of natural scenes.

A further body of research has examined the outer part of the receptive field (the extra-classical region) and the effect that stimuli placed in this region have on cell response. The extra classical receptive field has generally been shown to be suppressive in its effect on the cell response to an optimally defined stimulus placed centrally within the receptive field (Blakemore and Tobin, 1972). Studies have also shown that this suppressive effect may be limited to certain parts of the area (Walker et al., 1999). Researchers have attempted to address the spatially asymmetric nature of cell modulation by examining the effect of placing stimuli at various points within the extra classical receptive field.

Experiments have therefore examined the effect of placing stimuli at regular intervals within the classical receptive field. The orientation and temporal frequency of these stimuli has also been varied. Results have shown that specific locations in the extra classical receptive field can have a greater suppressive effect on the cell response than others, and the maximum suppressive effect is achieved using stimuli that have similar spatial and temporal properties to the optimal stimuli used to drive the classical receptive field (Walker et al., 1999, Walker et al., 2000). There is a degree of debate concerning whether these effects are a product of lateral inhibition within V1 or due to feedback / feedforward connections from other anatomical areas.

The vast proportion of work that has examined the modulatory effect of placing stimuli in the extra classical receptive field has done so by placing stimuli along the axis of orientation of a receptive field in the 'end zones' (Hubel and Wiesel, 1965, Orban et al., 1979, Deangelis et al., 1994, Li and Li, 1994). Such work shows that the receptive fields of V1 cells fall into two types; those that are end-stopped and those that are non-end stopped.

Functionally these receptive field types could be beneficial in detecting the termination of a line segment (Julesz, 1981) or the detection of illusory contours (Peterhans and von der Heydt, 1991) . Such spatial selectivity could be of use in the detection of acute or obtuse angles or curvature. The study of the modulatory effects of stimuli placed in the extra classical receptive field therefore has important functional and theoretical implications and further work is required to make apparent the degree to which V1 cells exhibit these properties.

Another area where extra classical effects are of interest is the chromatic properties of the extra classical receptive field. Chromatic modulation has been shown to affect the response to achromatically responsive cells when chromatic and achromatically modulated gratings are presented within the classical receptive field (Derrington et al., 2002). Further study has therefore examined whether the 'context effects' of stimuli placed in the extra classical surround extend to stimuli that contain chromatic information.

Chromatic stimuli have been shown to suppress cell response (when placed in the extra classical surround), however to a lesser extent than achromatic stimuli (Solomon et al., 2004). In this chapter I used stimuli placed in the outer part of the receptive field to address the effect of achromatic and chromatic flanking stimuli. The flanking ellipses did not cover the entire field. Questions therefore remain concerning whether or not a similar suppression effect is observed when using these types of ellipse stimuli as with the patch like stimuli that cover the entire extra classical receptive field. Specifically, I was interested in whether or not the modulation in response caused by the addition of both chromatic and achromatically varying ellipses was similar to the modulation in response caused by the addition of achromatic varying ellipses.

Functionally such an effect is of importance for several reasons. Shifts in response caused by the addition of chromatic surround stimuli could be implicated in the phenomenon of colour constancy (the influence of neighbouring regions of colour on the perception of a coloured patch). Colour constancy has been proposed to be of functional benefit in the detection of objects under the variant illuminations found in many natural settings. Context effects could also be of benefit in the segmentation of the visual image,

the comparison of regions of chromaticity is an important factor in the breaking up of the visual scene (Gegenfurtner, 1999).

In the previous chapter (Chapter 7), cells were shown to be differentially responsive, depending upon the specific combination of luminance and chromaticity present in the cells receptive field. In this chapter, I wanted to examine if this selectivity remained when the stimulus was extended outwards into the extra classical receptive field.

If however, the suppression in response caused by the addition of ellipse stimuli into the extra classical receptive field was great enough to impede cell response to a level where selectivity was lost then it would be of relevance as cells would be responding in a selective way for stimuli that were restricted to the classical receptive field and an unselective way if stimuli extended into the extra classical receptive field. This could be of functional relevance, as the cells would be showing spatial and chromatic selectivity.

8.2 METHODS

The same methods and animals were used as detailed in the previous chapter (see Chapter 2 and Chapter 7).

8.2.1 Stimuli

All of the stimuli used within this chapter were based upon the single ellipse stimuli detailed in the previous chapter. Once the optimal achromatic ellipse stimuli had been defined, cells' were tested with the optimal achromatic ellipse stimuli placed centrally within the cells receptive field and various flanking ellipse of the same dimensions as the achromatic central ellipse placed at either end of the centrally located ellipse. The orientation of the flanking ellipses paced at each end of the central ellipse was varied so that the stimulus set shown in Figure 8-1 was produced. The flanking ellipse was therefore orientated at 0, 45, 90, 135, 180, 225, 270 and 315 degrees relative to the orientation of the central ellipse.

Cells were tested with 6 repetitions of all of the 16 combinations of central and flanking ellipse, as well as 6 repetitions of each of the flanking ellipses presented in isolation. Cell response was measured for each presentation of all of the above stimuli and then averaged over all repetitions of the same stimulus. Measures of the spontaneous firing rate were also taken, as well as measures of the response to the single centrally located ellipse.

For each cell the measures of cell response were analysed in order to select the flanking ellipses that, when added to the central ellipse, produced a maximal increase in response and a maximal decrease in response. Checks were made to ensure that the cell

response was produced by the combination of central and flanking ellipses rather than the flanking ellipses presented in isolation.

Having established the combination of ellipses that produced a maximal change in response (for both increases and decreases in firing rate) a further test was run to examine the effect of the addition of chromaticity to the ellipse pairs that maximally modulated cell response. All stimuli that were used in the test contained luminance modulation that was in phase for both the central ellipse and the flanking ellipse. All stimuli that contained chromatic variations also contained achromatic variations such that the elevation of the DKL vector spanned between –45 degrees and 45 degrees (as in the previous chapter, for more information see Chapter 2). All stimuli that were chromatically modulated utilised an axis of modulation along the constant LM DKL axis. Two types of chromatic stimuli were used, these both contained chromatic and achromatic modulation that was in phase for the central and flanking ellipses. The chromatic specifications of the ellipses were varied so that stimuli consisted of:

1) Ellipse pairs where increases in luminance were accompanied by yellow-ward shifts in chromaticity and decreases in luminance were accompanied by blue-ward shifts in chromaticity.

2) Ellipse pairs where decreases in luminance were accompanied by yellow-ward shifts in chromaticity and increases in luminance were accompanied by blue-ward shifts in chromaticity.

Data analysis

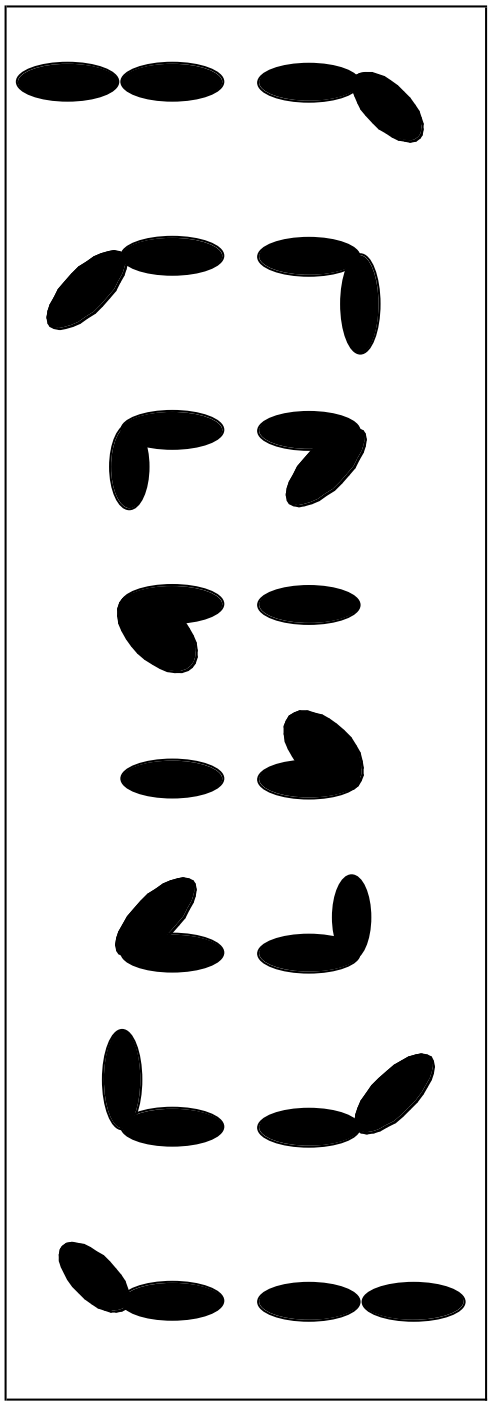

Figure 8-1: Example of stimulus set (achromatic)

The same criteria for classifying cells into simple and complex types were used as the previous chapter. The same discard criteria were also used (cells producing a discharge rate or < 5 spikes/sec). Data was analysed using the functions in the stimulus presentation program (EXPO) and MATLAB.

8.3 RESULTS

8.3.1 Cell response is modulated asymmetrically by the addition of achromatic flanking ellipses

The aim of this chapter was to discover whether or not the response of V1 cells to the optimally defined ellipses detailed in the previous chapter was affected by the addition of another similar ellipse placed in the surrounding area of the cells receptive field. A second ellipse was added so that the ends of the central and flanking ellipses were located in the same position. This was the same technique that was used to create the flower-like objects detailed in the general methods.

Recent findings suggested that cells in V1 would show a modulation in response based upon the addition of the secondary 'flanking' ellipse. If cells were found that showed a significantly larger or smaller response caused by the addition of a specific flanking ellipse (compared to the response for a singular ellipse) then V1 cells could be shown to be influenced by combinations of ellipses, this would have important implications for theories of V1 function.

Figure 8-2 shows an example of the cell response that was recorded upon presentation of various combinations of flanking ellipses (presented alone or alongside the optimally defined central ellipse). The plot shows the response from a simple cell in V1 (MA42M). Within the plot, the open circles represent the cells' response to the flanking ellipse presented in isolation. The plus and cross symbols represent the response to the flanking ellipse and central ellipse presented simultaneously (plus = flanking ellipse orientated at 90 degrees, crosses = flanking ellipses orientated at 0, 45,

135, 225, or 315 degrees). The horizontal blue line represents the response to the centrally located ellipse presented in isolation.

As can bee seen from the figure, the addition of the flanking ellipses generally produced suppression in the cells response. This is what would be expected from general theories of the receptive field profile in V1. The flanking ellipses were also presented in isolation in order to ensure that the cell response was a product of both central and flanking ellipse. If the flanking ellipses that were orientated away from the cells receptive field had produced a response when presented in isolation, then it would have meant that the central ellipse was not positioned correctly. In the case of the cell depicted by Figure 8-2, the stimuli were clearly positioned correctly, as no single flanking ellipse stimulus produced an appreciable cell response.

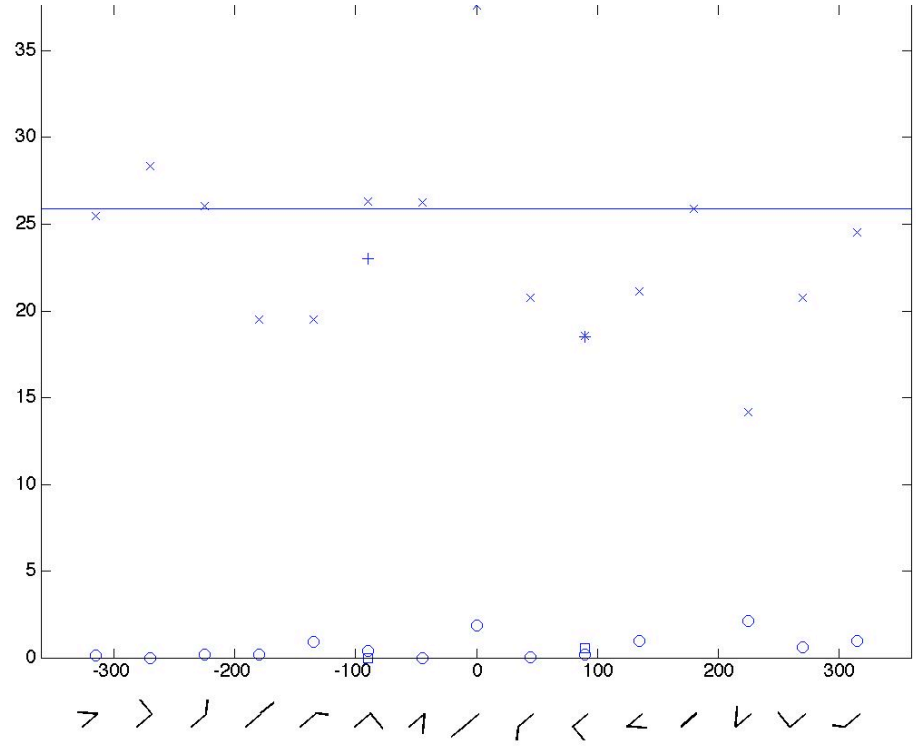

Figure 8-2: Example cell response for simple cell MA42M. The combinations of lines plotted below the x-axis represent examples of the stimuli used within the experiment. Each combination of lines refers to the data point (the crosses) situated directly above the lines. Although combinations of lines were used for convenience within the figure, the experimental stimuli consisted of combinations of ellipses. See text for more details.

In order to assess the comparative effect of single and multiple ellipse combinations, the same population of cells were used as detailed in the previous chapter. The optimal centrally positioned ellipse was defined and then a further test was run in order to assess the affect of the addition of flanking ellipses. Cells were classified as to whether they were simple or complex (see general methods). Two cells were rejected from the population because their response for all of the combinations of ellipses was below 5 spikes/sec or 5 impulses/sec.

Figure 8-3 to Figure 8-5 show a selection of the types of response observed over the population of cells. Within each plot the bars are shaded dependent upon the cell response to one of the stimuli used within the experiment. Within the figures, bars were used to depict the combinations of ellipses used: the stimuli used within the experiment were all ellipses.

The bars were shaded based upon the response of the cell to a specific combination of ellipses. For simple cells the shade was based upon the cells average FT amplitude (for a specific stimulus), extracted at the optimal temporal frequency. For complex cells the shaded colour represented the cells average spike count (for a specific combination of ellipses). Blue shades represented an inhibition of cell firing compared with the cell response to the centrally located ellipse and red shades indicated an excitation of cell firing compared to the response to the centrally located ellipse

The centrally positioned bar represented the response to the centrally located ellipse, the flanking bars represented the response to the combination of the centrally located ellipse and one of the flanking ellipses. As can be seen from the figures, cells were found that showed general inhibition in their response to all combinations of central ellipse and flanking ellipses, selective inhibition to some of the combinations of the central ellipse and the flanking ellipses and selective inhibition and selective excitation for the combinations of the central ellipse and the flanking ellipse

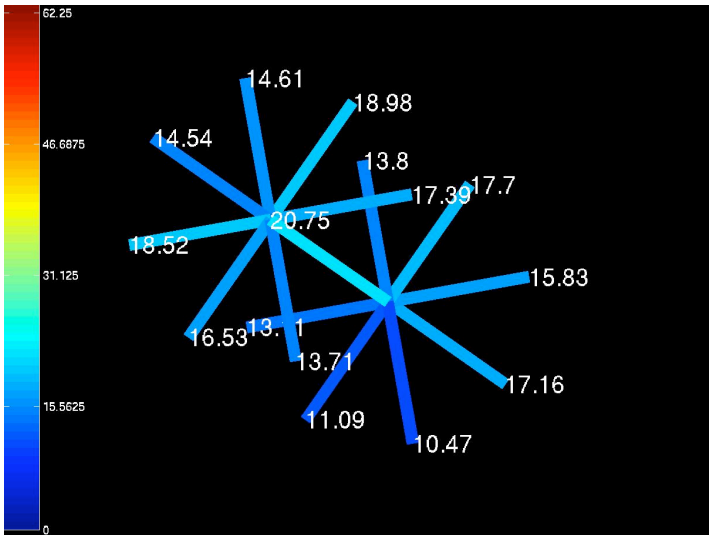

Figure 8-3: Cell response from simple cell MA42F. Centrally positioned bar represents the cell response to the centrally positioned ellipse. All other bars represent the cell response to the combination of central and flanking ellipse. The cell showed a general inhibition of response when flanking ellipses of any orientation were added.

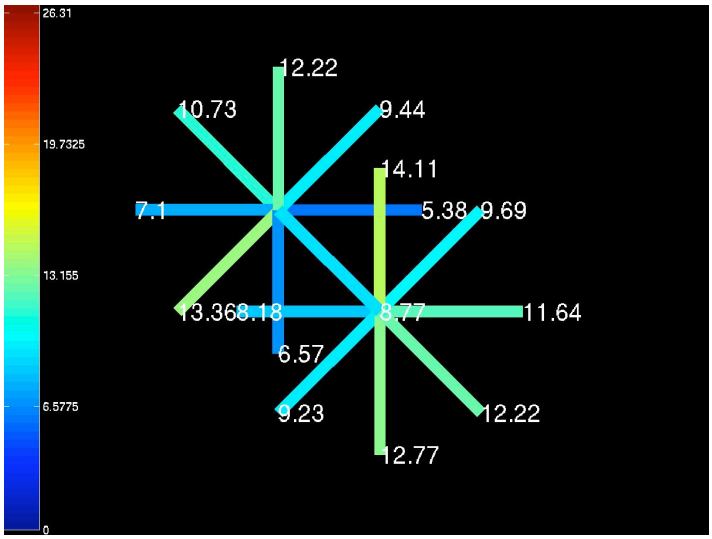

Figure 8-4: Cell response from complex cell MA40C. The cell shows a general increases in response (compared with the response to the singular centrally located ellipse) when flanking ellipse that are orientated away from the receptive field are added.

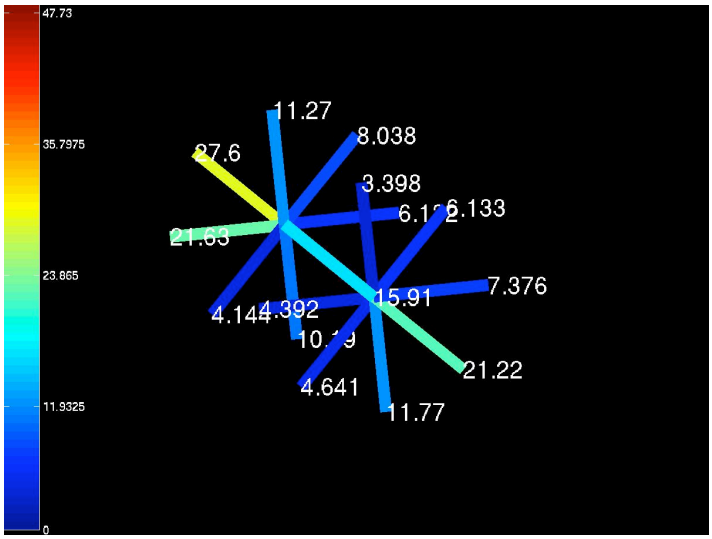

Figure 8-5: Cell response from simple cell MA41K. The cell shows increases and decreases in response due to the addition of various flanking ellipses. This was dependent upon the orientation of the flanking ellipse.

I wanted to establish the degree to which each cell within the population of cells showed a modulation in response caused by the addition of flanking ellipses. Comparative measures were therefore taken for the combination of central ellipse and flanking ellipse that maximally increased cell response and maximally decreased cell response (compared to the response of a single centrally located ellipse). By comparing the cell response to the singular centrally located ellipse and the combination of centrally located ellipse and flanking ellipse it was possible to obtain an index of how much the cell response was affected by the addition of flanking ellipses. This index was calculated for the combination of central and flanking ellipse that produced a maximum increase and a maximum decrease in cell response (compared to the response to the singular centrally located ellipse).

Values of modulation were calculated by dividing the cells maximal and minimal response by the response for the centrally placed ellipse. The obtained value tended

towards 0 for very large decreases in response and tended towards 100 for very large increases in response. For example if the response to the centrally located ellipse was 10 spikes/sec and the addition of one type of flanking ellipse caused the cell to fire at 50 spikes/sec and another type of flanking ellipse caused the cell to fire at 5 spikes/sec then the modulation in response for the increase would be 5 and the modulation in response for the decrease would be 0.5.

The log of the modulation values was then calculated. The sign of the log value revealed if the value of modulation was produced by an increase or decrease in response. For negative log values, the modulation in response was a product of a decrease in firing and for positive log values the modulation in response was a product of an increase in firing.

Figure 8-6 shows the comparative log values for the combination of ellipses that produced maximal increases and decreases in firing. As can be seen from the figure all points plot in the bottom right hand quadrant, as would be expected from the classification system. As can be seen in Figure 8-6, specific combinations of ellipses tended to produce a greater decrease in response than increase in response as most of the points plotted near or around the y-axis.

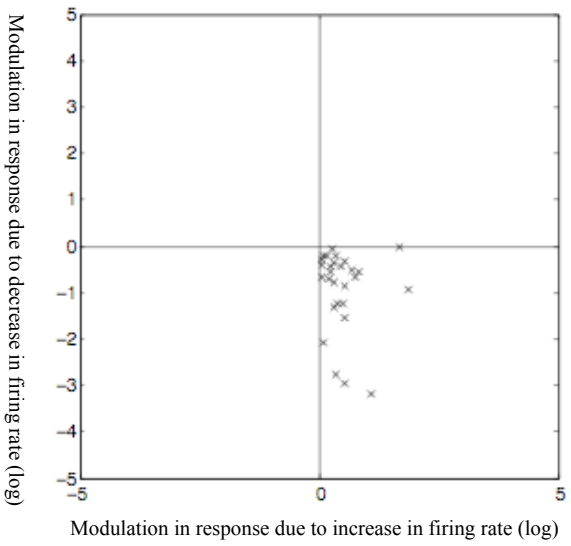

Figure 8-6: The log of the modulation in response caused by the addition of flanking ellipses that produced a maximal increase or decrease in response.

In order to assess if the changes in response were statistically significant, analysis was conducted using Bonferonii corrected t-tests. The response to the centrally located single ellipse stimuli was compared to the cell response provided by the presentation of the two ellipse combinations.

Of the 28 cells included in the analysis, 13 were classed as simple and 15 were classed as complex. 4 cells displayed a significant inhibition caused by the addition of a flanking ellipse, they therefore showed a significantly smaller response when the inhibitory flanking ellipse was added to the centrally located ellipse but showed no significant change in response when the excitatory flanking ellipse was added to the centrally located ellipse.

4 cells showed a significant excitation due to the addition of a flanking ellipse. They provided a significantly greater response for the excitatory flanking ellipse but no

significantly different response for the inhibitory ellipse. 1 cell showed both excitation and inhibition caused by the addition of a flanking ellipse.

In conclusion, cells showed a modulation in response caused by the addition of a flanking ellipse that could be excitatory or inhibitory. Of the cells surveyed 9 showed a significant modulation in response. It is therefore suggested that cells in V1 can show a degree of selectivity for configurations of ellipses that are similar to the hypercomplex stimuli first described by the pioneering studies of cat striate cortex (Hubel and Wiesel, 1962).

8.3.2 For a given cell, modulation in response is altered when the stimuli used to drive the cell contain chromatic variations.

In the previous section 8.3.1 it was demonstrated that the addition of an achromatic flanking ellipse of a specific orientation could significantly alter the response of a cell to a centrally placed optimally defined ellipse. Modulations in response could be both increases and decreases in response and were found to be specific to a certain orientation of flanking ellipse.

I was interested in whether or not a similar effect was observed when ellipses that contained a mixture of chromatic and achromatic modulation were used to drive cells. Specifically, I wanted to know if for a given cell the modulation in response was of similar direction and magnitude to the modulation is response observed for the achromatic ellipses.

In order to assess whether the chromatic properties of the combination of central and flanking ellipse affected the way in which the addition of a flanking ellipse

modulated response, the combination of central and flanking ellipses that caused the maximum facilitation and suppression in response were tested using chromatically and achromatically modulated stimuli. Examples of these types of stimuli are shown in Figure 8-7. As with the chromatically and achromatically modulated single ellipse stimuli (detailed in the previous chapter), two classes of chromatically and achromatically modulated double ellipse stimuli were used. One type of stimulus contained yellow ward modulation that accompanied increases in luminance and blue-ward modulation that accompanied by decreases in luminance. The other type contained yellow-ward modulation that accompanied decreases in luminance and blue-ward modulation that accompanied increases in luminance.

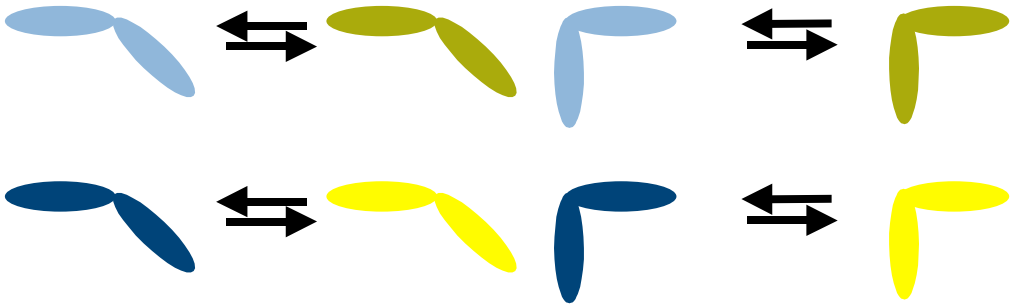

Figure 8-7: Examples of the stimuli used to test the response to combinations of ellipses containing chromatic and achromatic information. Top row = increases in luminance accompany blue-ward shifts in chromaticity. Bottom row = decreases in luminance accompany yellow-ward shifts in chromaticity. Right hand pair of ellipses = example of ellipses that produce a maximal increase in response when rendered achromatically. Left hand pair of ellipses = example of ellipses that produce a maximal decrease in response when rendered achromatically.

Figure 8-8 shows the combinations of ellipses that produced a maximum facilitation in response and a maximum suppression of response when achromatically defined flanking ellipses were added to an achromatically defined central ellipse. The corresponding cell PSTH is provided above the example stimulus, this depicts the time course of the cell response over two stimulus cycles. As can be seen from the figure, the cell increases its response when the excitatory flanking ellipse is positioned within the surround and decreases its response when the inhibitory flanking ellipse is positioned within the surround.

The figure also shows the PSTH's for cell response to stimuli consisting of the same configurations of ellipses but with chromatic and achromatic properties. The chromatic variations within the stimuli were in phase and decreases in luminance were accompanied by yellow-ward shifts in chromaticity and increases in luminance were

accompanied blue-ward shifts. This colour condition was depicted as it produced the maximum modulation in response.

As can be seen from the figure a similar type of modulation in response was observed for the combinations of ellipses that contained achromatic and chromatic variations, as was observed with the ellipses that contained only achromatic variations. For this cell the chromatic and achromatically defined ellipses produced increases or decreases in response of a similar magnitude compared to the effects observed with achromatically defined ellipses. For a subset of the cells, differential effects of adding the same flanking ellipse were observed between the stimuli that contained and did not contain chromatic information (Figure 8-9)

In some cases, modulations in response were observed with achromatically defined stimuli that were not observed with achromatically and chromatically defined stimuli. In other cases an increase in response for achromatically defined ellipses was noted where for the same cell a decrease in response for achromatically and chromatically defined ellipses was recorded (and vice versa).

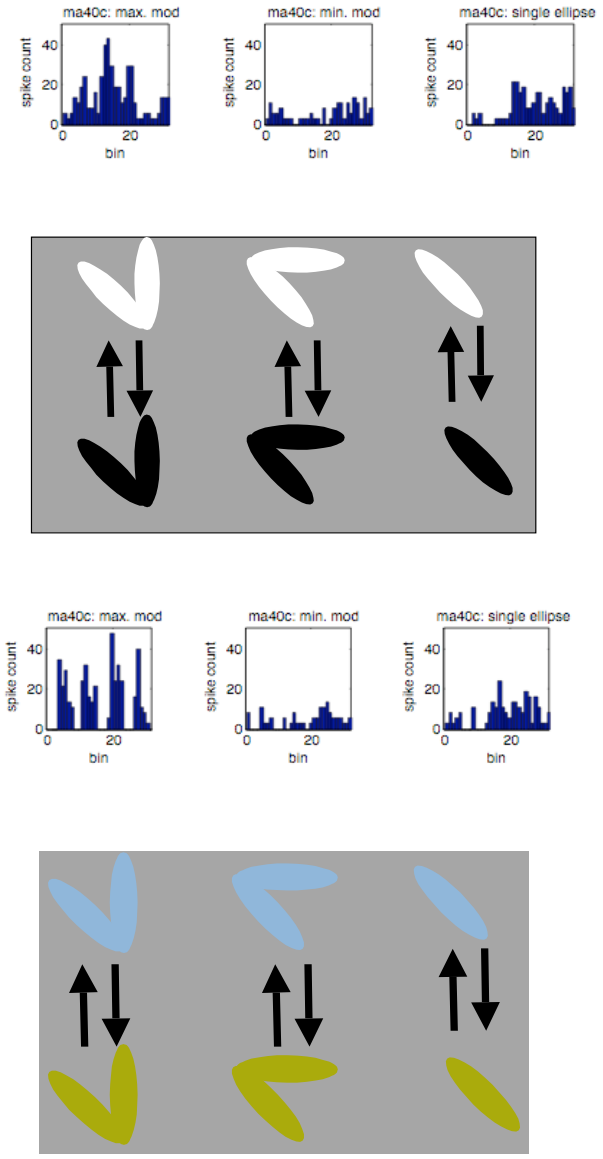

Figure 8-8 Example cell response from MA40C. Top row = PSTH's for the response to the depicted achromatically modulated ellipses. Left hand box = the combination of ellipses that produced a maximal increase in cell firing. Middle box = the combination of ellipses that produced a maximal decreases in cell firing. Right hand box = the response to the single centrally placed ellipse. Second row PSTHS, the equivalent response, but for stimuli that contained achromatic and chromatic modulation.

Figure 8-9 shows the response of a complex cell in V1. As can be seen from the PSTH charts, the addition of achromatically modulated flanking ellipses caused a shift in response that was different to the shift in response caused by the addition of chromatically modulated flanking ellipses. Both types of chromatically modulated flanking ellipses caused a decrease in response.

The majority of cells (13/30) showed no significant change in response caused by the addition of either excitatory or inhibitory ellipse combinations for stimuli that did or did not contain chromatic information. Four cells showed a significant decrease in response caused by the addition of achromatically modulated flanking ellipses but showed no significant change in response when the same stimulus contained chromatic information. Four cells showed a significant increase in response caused by the addition of an achromatic flanking stimulus, again no significant change in response was observed when chromatic stimuli were used. One cell showed a significant decrease in response caused by the addition of a flanking ellipse containing chromatic information that was not observed for the same stimulus that did not contain chromatic information.

In conclusion the presence of chromaticity within the flanking ellipse had an effect upon the way in which the flanking ellipse modulated cell response. It was generally shown to be the case that stimuli containing chromatic information did not produce a significant change in response, where achromatic stimuli did. In 1 out of 30 of the cells a significant modulation in response caused by the addition of flanking stimuli was observed for stimuli containing chromatic information where it was not observed for stimuli containing only achromatic information.

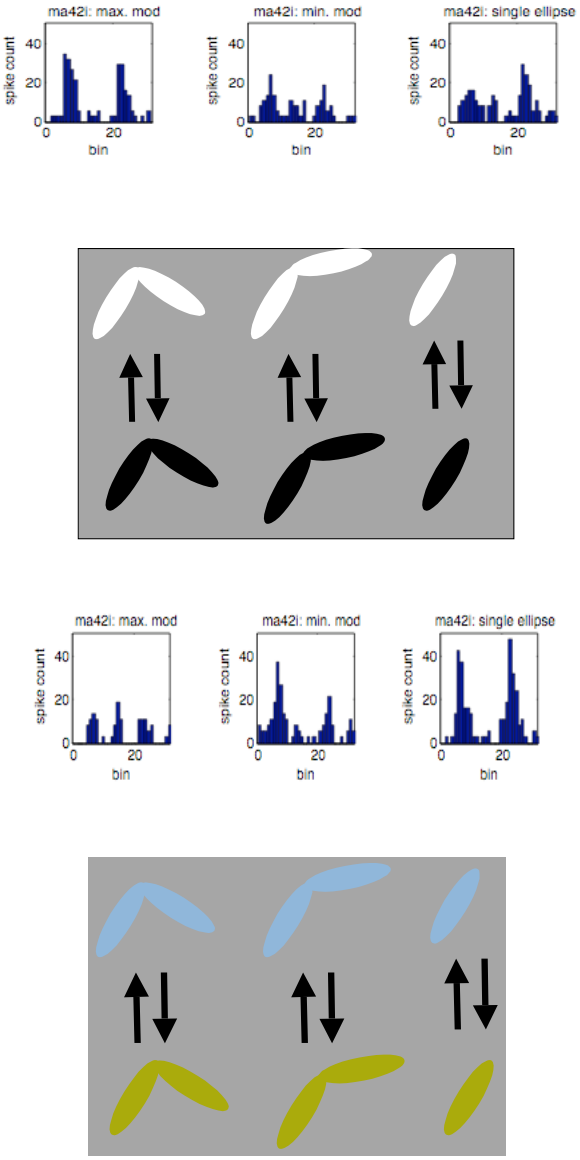

Figure 8-9 Example cell response from MA42I. Top row = PSTH's for the response to the depicted achromatically modulated ellipses. Left hand box = the combination of ellipses that produced a maximal increase in cell firing. Middle box = the combination of ellipses that produced a maximal decreases in cell firing. Right hand box = the response to the single centrally placed ellipse. Second row PSTHS, the equivalent response, but for stimuli that contained achromatic and chromatic modulation.

8.3.3 Modulation in response is dependent upon the combination of luminance and chromaticity within the stimulus.

The ellipses that contained chromatic information were presented in two ways. In one set of stimuli, increases in luminance accompanied yellow-ward shifts in chromaticity and decreases in luminance accompanied blue-ward shifts in chromaticity. In the other set of stimuli increases in luminance accompanied blue-ward shifts in chromaticity and decreases in luminance accompanied yellow-ward shifts in chromaticity. I wanted to examine if the cell response for the two-ellipse stimuli showed a similar tendency to provide a differential response when specific changes in chromaticity were accompanied by increases in luminance versus decreases in luminance. Such differences were of interest as they would indicate that response was a product of the chromatic elements of the stimulus as well as the achromatic elements of the stimulus and suggest a combined selectivity for colour and luminance.

In a subset of the cells the addition of flanking ellipses had significantly different effects on cell response dependent upon the type of chromatic flanking ellipse that was used. This difference is illustrated in Figure 8-10. Here the addition of a flanking ellipse that contains the same chromatic and achromatic modulation as the central ellipse (blue-ward modulation accompanied by decreases in luminance, yellow-ward modulation accompanied by increases in luminance) causes a significant facilitation in response (Bonferonii corrected t-test). The addition of a flanking ellipse that contained decreases in luminance accompanied by yellow-ward shifts in chromaticity and increases in luminance accompanying blue-ward shifts caused no significant change in response.

This differential effect showed that the chromatic content within the ellipses was responsible for driving cell response. It also showed that the cell was selective for a combination of luminance and chromaticity. Of the 30 cells surveyed two showed a response that could be described in a similar way. Both of these cells showed a selective response for yellow-ward modulation being accompanied by increases in luminance compared to yellow-ward modulation being accompanied by decreases in luminance. The stimuli that contained increases in luminance accompanied by yellow-ward shifts in chromaticity only caused modulations in response that were facilitating in nature and the stimuli that contained increases in luminance that were accompanied by blue-ward shifts caused modulations in response that were facilitating and inhibitory in nature. This meant that the addition of yellow chromatic information was causing cells to fire to a greater extent than for the single ellipse stimuli, for both combinations of ellipses that caused an increase in firing.

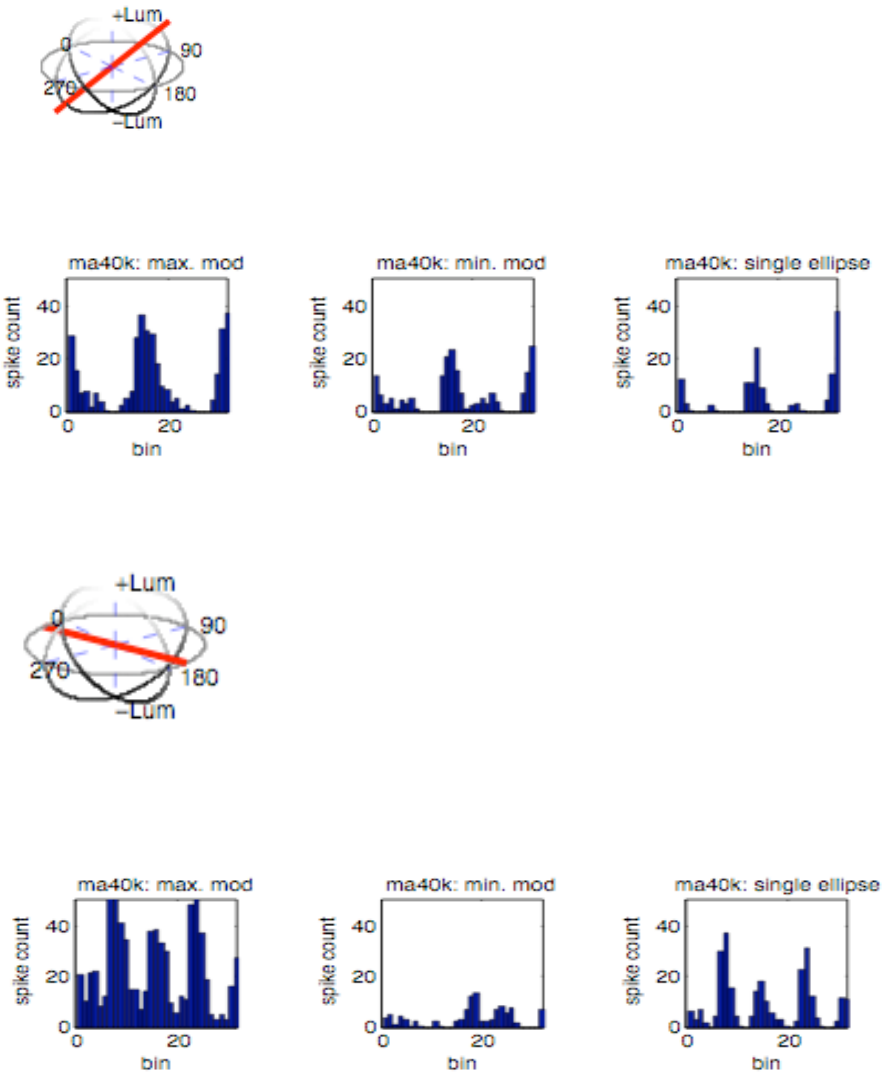

Figure 8-10: Comparison of cell response for the same combinations of ellipses shaded in the two chromatic conditions. Response from cell ma40k, also depicted in figure 5. Left hand box, facilitatory chromatic and achromatically modulated ellipse combinations. Middle box, inhibitory chromatic and achromatically modulated ellipse combinations. Right hand box single chromatic and achromatically modulated ellipse. Top row = increases in luminance accompanied by blue-ward modulation. Bottom row = increases in luminance accompanied by yellow-ward modulation.

DISCUSSION

In conclusion ellipses placed outside the classical receptive field of V1 cells were shown to have a significant excitatory and / or inhibitory effect on cell response and this was shown to be specific to a certain combination of central and flanking ellipse. Such effects were also observed when chromatically and achromatically modulated stimuli were used to drive cells. For a few of the cells, cell response was shown to be differentially modulated depending upon the direction in colour space of the chromatic modulation.

Possible limits to the study include various spatial factors concerning the definition of the optimal stimulus. Although tests were employed to ensure that the optimal ellipse stimulus was placed centrally and extended to the limits of the classical receptive field, if the receptive field profiles were atypical (curved, or contained orientation discontinuities), then the test that I employed was not providing a complete characterisation of the cells receptive field. Further work is required to address this issue. The benefit of using such stimuli is that they approximated the features used in the flower type stimuli detailed in Chapter 4 - Chapter 6 .

The finding of atypical receptive field profiles for marmoset V1 neurons was of interest for a number of reasons. In many of the cells surveyed, the combination of ellipses that were found to maximally drive cell response contained orientation discontinuities. These would be of use in the detection of corners, edges or curvature. Several other studies (recording in cat V1) have found cells that are driven by these types of stimuli (Shevelev et al., 1994, Shevelev et al., 1999, Shevelev, 1999) and the original study of the spatial characteristics of V1 cells termed a class of hypercomplex

cells that responded to lines of specific length or combinations of lines (Hubel and Wiesel, 1962). Investigations with plaids (in the marmoset) have also shown that a subset of neurons show a response based upon the combination of components (compared to other neurons which respond to the components of the plaid) (Tinsley et al., 2003).

Based upon these findings, V1 in the cat and the primate has been shown to contain the cortical apparatus to signal changes in light intensity that are present in edges, angles corners and bars. Although a very small subset of the cells found fitted into the class of cells originally defined as hypercomplex, such cells exist and are functionally important in the representation of the visual image. Models of visual perception would therefore be more plausible if they utilised basis functions that approximate the filtering characteristics of the above cells. Such models have been proposed by authors (Fukushima, 1980, Skottun, 1998, Riesenhuber and Poggio, 1999), however further work is required to examine the precise role that hypercomplex cells play in the visual process.

The chromatic properties of the neurons that were surveyed were also of interest. Far fewer cells showed a significant modulation in response caused by the addition of chromatically modulated ellipses than they did for the achromatic ellipses. This result converges upon that of Solomon and colleagues (Solomon et al., 2004), where smaller shifts in cell response to optimal stimuli were observed for the addition of chromatic compared with achromatic extra classical stimuli.

The fact that stimulation of the outer part of the receptive field produces a significant modulation in far fewer cells than with achromatic stimuli has functional

relevance for the comparative utility of the chromatic visual information compared with achromatic visual information. Proposals of hypercomplex ‘’feature detectors’ based upon findings with achromatic stimuli have yet to be conclusively extended to the domain of chromatic stimuli. Few of the cells surveyed showed significant modulation in response caused by the addition of chromatically modulated ellipses, and in many cases the modulation in response was in a different direction to the modulation in response caused by the addition of the same achromatically modulated ellipse.

Two questions arise from the results. Firstly why would a hypercomplex unit signal a different modulatory effect when stimulated with achromatic and chromatic stimuli? Secondly what would the likely mechanism that would lead to this response involve? Differential modulation between chromatic and achromatic stimuli could reflect the differing functional uses of the visual information. In the case of stimulus chromaticity the influence of neighbouring regions has been shown to directly effect the perception of the colour (e.g. colour constancy), and this mechanism has been shown to be of importance in visual perception. For achromatic stimuli, the relative intensity of neighbouring regions is of less functional use, more important is the fact that a difference in intensity exists.

Accounts of the mechanisms underlying the modulation of cell response due to the placing of stimuli in the extra classical receptive field suggest that feedback connections from extra striate cortex are responsible for the spatial scale of the surround field (Angelucci et al., 2002). Such connections have been shown to be both excitatory and inhibitory in nature (Bullier et al., 1996). However in the case of this study, as the central stimulus did not cover the entire of the classical receptive field, it is possible that

local horizontal interconnections could account for the phenomenon involved (Stettler et al., 2002). In both cases, connectivity could lead to an increase or decrease in cell response, however it is more likely that differential modulations in response would arise from extra striate feedback, further study is required to clarify the issue.

Despite the small number of cells that were discovered in this study, other studies have reported chromatically sensitive hyper-complex cells in monkey striate cortex (Michael, 1979), it is therefore concluded that such cells exist in primary visual cortex and are utilised by the visual process.

Why does our study fail to find large numbers of these cells? One possible reason for the discrepancy between this study and others was the fact that some of the animals used in this study were dichromatic. The majority of previous studies have been performed in trichromatic macaques. Such an issue is of importance as fMRI studies have shown a bias in the level of cortical activity in human striate cortex towards stimuli that are restricted to the red-green cortical pathway. This pathway would have been deficient in the dichromatic marmosets that were used. Further recording studies are therefore required using a type of stimulus detailed in this chapter but in macaque monkeys.

Having shown in the previous chapter that cell response to single optimally defined ellipses was dependent upon the direction in colour space that the ellipse was rendered in, conformation of this finding was established using the two ellipse stimuli described in this chapter. Studies that have examined the effect of extra classical stimuli on cell tuning to chromatic stimuli placed in the classical receptive field showed no change in their chromatic tuning to stimuli placed within the classical receptive field

(Solomon et al., 2004). This is further confirmed by the fact that in this study cells were shown to be selectively for a particular direction of colour space irrespective of whether or not a one or two ellipse stimulus was used. Further study is required to establish a complete specification of the chromatic selectivity of marmoset V1 receptive fields and how this selectivity is combined with the spatial profiles of the receptive field.

Chapter 9 CONCLUSION

9.1 INTRODUCTION

In this thesis, I examined the contribution that colour provides to visual processing, at behavioural and physiological levels in human and non-human primates. In the introduction, I outlined several areas where I believed further research was required to clarify theories of chromatic function. These were:

Does stimulus colour advantage human object recognition and is any advantage specific to colours convey by either of the two chromatically opponent pathways?

Does stimulus colour advantage macaque object recognition and is any advantage specific to colours conveyed by either of the two chromatically opponent pathways?

Does stimulus colour advantage the object recognition abilities of dichromatic marmosets?

Is it possible to use elements of naturalistic objects (ellipses) to drive single neurons in anesthetised marmoset V1?

Are similar numbers of V1 cells taken from the same population found that provide a significant response when the ellipse stimuli contain chromatic and achromatic modulation compared to stimuli that only contain achromatic modulation?

Is cell response modulated (compared to the response for a single optimally defined ellipse element) when combinations of ellipses are used that approximate feature- like stimuli?

Are similar modulations in response found when the feature like stimuli contain chromatic modulations as well as achromatic variations?

In this chapter I intend to review the results that were obtained relating to the above questions, compare them to results previously reported in the literature and contrast the findings in order to provide a general theory of the contribution of colour to the visual stream.

9.2 REVIEW OF RESULTS

In the first sections of the thesis (Chapter 3 and Chapter 4), studies with human subjects revealed a deficit in object recognition memory caused by the removal of chromatic information. The deficit was observed to be largest when there was a short delay interval between study and test object. This suggested that chromatic information provided an advantage in object recognition, and was manifest at a sensory level. High level cognitive processes were excluded from contributing towards the observed effects

as the type of object used provided little information with which to use diagnostic cues (they contained a high level of feature ambiguity).

Further analysis revealed that a deficit in ability was caused by the removal of red-green chromatic modulation but not blue-yellow chromatic modulation from the object stimuli. This suggested that the sensory-based advantage provided by chromatic information was predominantly conveyed along the red-green chromatically opponent pathway. When subjects were tested with objects that lacked all achromatic information, their recognition ability was not significantly reduced, further highlighting the fact that colour provides a facilitation over and above that of achromatic variations in human object recognition.

In the second sections of the thesis (Chapter 5 and Chapter 6), a similar test was conducted using macaque monkeys. I found that colour facilitated macaque list learning ability and that the removal of red-green chromatic information impaired recognition ability (compared to the removal of blue-yellow) when data from the first session of each list was analysed. These results were similar to the results found in human subjects. This difference was also reflected in the reaction time provided by the macaques when responding to object discrimination pairs. I also discounted the possibility that differences in the stimulus conditions were a product of the structural elements of the objects, by examining the within condition variability.

Further study using dichromatic marmosets also showed an impairment in discrimination ability when chromatic information was subtracted from similar object stimuli. This was an unexpected finding. Based upon the results from human subjects and old world primates, it was expected that the s-cone opponent system had a minimal

influence upon object recognition. The presence of a deficit in object recognition abilities in dichromatic marmosets caused by the removal of chromatic information therefore contradicted this result, as all chromatic information was conveyed along the s-cone opponent pathway in these animals.

Contrast and structure were shown to have a minimal influence upon the visual discrimination ability of the marmosets. It was therefore concluded that marmosets were utilising chromatic information in their visual recognition abilities and the s-cone system was implicated in this ability.

The final sections of the thesis (Chapter 7 and Chapter 8) examined the neuronal underpinnings of the processing of object shape and colour by testing cells in marmoset V1 with simple feature like stimuli. I found that cells showed a significant response for single ellipse stimuli, of the type that were used to construct the objects that were used to test behavioural abilities. When the direction of modulation in colour space was changed so that the stimuli contained chromatic and achromatic modulation, far fewer of cells (taken from the same sample) showed a significant response.

In order to further explore the spatial selectivity of the cells in marmoset V1, I tested the same sample of cells with various combinations of two ellipse stimuli. These approximated object features such as right angles, corners and edges. I found that cells showed significantly different responses when additional flanking ellipses were added. These modulations in response were also present for stimuli that were structurally identical but contained chromatic and achromatic modulation.

Based upon these finings is was suggested the marmoset V1 contained cells that responses were modulated by feature like stimuli, however very few of these cells

showed significant responses when stimuli of this types also contained chromatic modulation. Of the cells that did, a degree of chromatic selectivity was observed, however as the sample size was small further research is required to elaborate upon the role of the chromatic content of stimuli in V1.

9.3 HOW AND WHY DOES COLOUR PROVIDE A SENSORY ADVANTAGE TO OBJECT RECOGNITION?

My results with human subjects provide evidence that colour is giving an advantage at a fundamental level of the visual process. This is shown by the fact that recognition ability is reduced when chromatic variations are removed from naturalistic objects. This adds to findings that show a similar contribution of colour to the recognition of natural scenes (Wichmann et al., 2002), faces (Yip and Sinha, 2002) and pictorial objects (Homa and Viera, 1988). Some authors have also proposed that colour contributes to the visual process at higher cognitive levels (for example in object diagnosicity) (Tanaka and Presnell, 1999). Although these results does not exclude this possibility it shows that colour provides a sensory advantage in object recognition.

As the majority of mammals have some form of chromatically enabled vision, and colour provides a relatively stable way of segmenting the visual image (Healey, 1989), it seems unlikely that the visual system would only rely upon achromatic information in the representation of the visual world. Under isochromatic conditions vision has been shown to be relatively poor (Gregory, 1977). As the combination of chromatic and luminance variations within objects is ubiquitous in the natural environment it follows that a visual system that can utilise both of these factors at a relatively fundamental level is going to be able to discriminate a wider variety of

objects. Colour has been shown to provide various additional cues that are of benefit to the visual system in this respect (Kingdom, 2003).

Given that I proposed the effects of colour subtraction in humans were sensory in nature, a degree of justification is required relating to why the serial recognition task that was detailed in chapters 3 and 4, provided appropriate measures. The type of stimulus that was used was designed to be non-nameable and contain no nameable features.

Similar types of stimulus have been used by other object recognition studies. These include simple line based stimuli, fractal stimuli and geon stimuli (Parker et al., 1998, Hayward and Tarr, 1997, Poggio and Edelman, 1990). As with all of these types of stimuli, the features within the stimulus are ambiguous and are designed so that subjects will have no previous experience with the objects. The presentation time was also reasonably short and fixed so that subjects could not develop a strategy to encode the objects using mnemonic techniques.

Further justification for the above effects being sensory in nature is that the effects were present at short delay intervals between study and test objects. If subjects were using an explicit strategy to encode object based information, and the chromatic effects were dependent upon this, then I would expect them to span all delay intervals used.

Unfortunately human subjects tend to be naturally drawn to attributing verbal labels to ambiguous stimuli, and even with the large numbers of very similar objects that were provided in the serial recognition experiments, I can not rule out the possibility that some form of higher level memory based process was being used to encode the stimuli. As the human subjects progressed through the serial recognition task they tended to get

better at recognising similar types of objects and so future research could exclude this possibility by ensuring steady state memory conditions were achieved (as in (Shepard and Teghtsoonian, 1961)) or employing controls to counter this possibility.

Previous studies that have examined the contribution of colour within natural scenes have used controls to rule out the contribution of stimulus saliency (Wichmann et al., 2002). Saliency is generally used to suggest that prior experience with a stimulus attribute leads to the attribute in question gaining behavioural relevance and then providing a behaviourally significant cue in the retention or detection of information relating to the stimulus. The role of salience in the low level aspects of the visual scene has been investigated, researchers have examined effect of orientation, colour motion and luminance on visual search tasks and have found that the chromatic content of an object has a facilitatory effect on subject ability to detect search targets (Nothdurft, 1993).

In the studies detailed in chapters 3-6, the possibility of any advantage provided by the presence of a specific colour was excluded by measuring subject sensitivity thresholds for the cardinal directions of colour space and then normalising with respect to this. Any advantage afforded by a specific type of chromaticity was therefore due to the combination of colour and structure within the objects. This technique has been previously employed to investigate low-level chromatic processing (Krauskopf et al., 1982), however to the best of my knowledge has not been previously applied to studies that use naturalistic objects. As all objects of the study test pairs were trial unique objects, subjects did not have any previous experience with the objects that were used in the studies.

9.4 WHAT IS THE FUNCTION OF TRICHROMATIC VISION?

Having found effects relating to the subtraction of chromatic information in humans, questions must emerge relating to the comparative role of colour in non-human primate species. Specifically the corresponding role of stimulus colour in dichromatic and trichromatic visual systems was considered.

In similar studies with macaques and dichromatic marmosets, a common deficit was found relating to the subtraction of stimulus colour. Such a finding was unexpected as theories of the function of trichromatic vision suggest that the red-green opponent pathway (non-existent in dichromatic marmosets) has become specialised for the type of object recognition task that I tested both species on (Regan et al., 2001).

In the case of the marmosets, a deficit in object recognition ability was observed when I removed all colour from the stimulus. This shows that the primordial s-cone pathway is supporting object recognition in some form. Such a finding relates to human studies) showing dichromatic observers not to be impeded in their scene recognition abilities compared to trichromatic observers (Gegenfurtner et al., 1998), As detailed in previous studies, these results show that dichromatic subjects utilise the primordial blue-yellow pathway in object recognition abilities. Dichromatic subjects therefore compensate for any reduction in ability that would be suggested by the lack of a red-green opponent pathway.

Further to this, the compensation in ability is likely to be made at a sensory level, as no studies have shown marmosets displaying complex cognitive functions (e.g. to be able to employ strategies for learning). Where studies have compared dichromatic and trichromatic marmosets, trichromatic subjects tend to show a recognition advantage

specific to certain colours (Caine and Mundy, 2000), however this may simply be due to an inability to discriminate between specific shades rather than any sensory advantage that colour may provide.

What implications do the above results have for our understanding of the contribution of colour to human object recognition? Human dichromats have been shown to be missing the ability to discriminate nearly one million colours (compared to human trichromats) (Neitz et al., 2001). This has been reported to impede various visual abilities such as visual search and visual recognition (Stewart and Cole, 1989). In this thesis, I found that non-human primate models of dichromatic vision showed an advantage in object recognition that was dependent upon chromatic information. This means that although dichromatic chromatic discrimination is limited, colour is still providing a sensory advantage in visual object recognition.

Despite the fact that I observed a deficit relating to the subtraction of chromatic information in the marmoset, in macaques and humans, the removal of blue-yellow information was not found to have an effect on object recognition ability. One possible explanation for this apparent discrepancy is that the s-cone pathway shows differing functional specialisation dependent upon species. Therefore the contribution that the primordial s-cone pathway and the more recently evolved red-green pathway may be dependent upon whether an animal processes two chromatically opponent pathways or a single chromatically opponent pathway.

The red-green opponent system provides a greater spatial resolution than the blue-yellow opponent system (Mullen and Kingdom, 2002) and is not prone to effects of chromatic aberration. I propose that when the visual system of trichromatic species does

not have to rely on blue-yellow opponency, it is therefore biased towards the superior red-green system. This could explain the differential effects of s-cone pathway related chromatic subtraction between the dichromatic and trichromatic species studied within this thesis.

Other studies have suggested that the contribution that colour provides is specific to the red-green and blue-yellow pathways and has been dictated by evolutionary pressures. Such theories suggest that the red-green chromatic pathway has become specialised to provide an advantage for frugivory behaviours (Regan et al., 2001). The findings in humans and macaques support these ideas. When I took red-green colour away from flower-like objects, recognition ability was reduced. Many naturalistic fruit objects have reflectance spectra that fit into the red-green range, and studies have shown that trichromatic vision is advantageous in this respect (Sumner and Mollon, 2000).

Theories of red-green colour being advantageous in the detection of (for example) fruit from foliage are normally contrasted with theories that maintain dichromatic vision still affords some advantage in object recognition behaviour (such as increased spatial resolution or the discrimination of vegetable greens) (Williams et al., 1991). The later of these viewpoints is also supported by the results found in this thesis.

The conclusion that I therefore come to based upon the above arguments is that the function of the opponent pathways is species dependent. In dichromats, who rely upon the primordial s-cone pathway for all chromatic ability, the pathway makes a contribution to the early low level sensory aspects of the visual process. By removing the variations inherent in this pathway then object recognition abilities are reduced. In macaques and humans, there is a second more developed red-green pathway, and the

low level sensory aspect of the visual process are preferentially based upon this higher resolution pathway.

9.5 HOW DO THE RECORDINGS FROM SINGLE CELLS INFORM THE CONTRIBUTION THAT COLOUR MAKES TO THE VISUAL PROCESS?

Having concluded that stimulus colour provided a sensory contribution to the visual process and that this was common to both dichromatic and trichromatic visual systems the final part of this thesis examined the neuronal selectivity that could support the sensory representation of the types of objects used in chapters 3-6. This was achieved by examining the way in which cells in V1 of the anesthetised marmoset responded to feature like stimuli. This was performed for objects that contained chromatic information and for objects that contained both achromatic and chromatic information. The number of responsive cells and the way in which cells fired for these different types of objects was then compared.

When combinations of two achromatically modulated ellipses were used a far smaller proportion of cells showed a significant selectivity for combinations of ellipses than found by studies addressing a similar question using line based stimuli in the cat (Shevelev, 1998). In our study, a small proportion of V1 cells were found to selectively represent the types of corner and edge that have been outlined as being essential to the formation of a behaviourally relevant representation of the visual world by cortical apparatus. Generally researchers propose that these 'hypercomplex' units can be found in V1 however recent research had begun to suggest that V2 cells as being more likely to represent this kind of feature (Hegde and Van Essen, 2000).

A possibility emerges that hyper complex cells or cells approximating hyper complex cells are also formed from a combination of LGN concentric cells. This would be possible if a spatially asymmetric combination of ON and OFF centre cells were combined. An alternative possibility is that neuronal activity pooled across the cortical area is affecting the cell response for stimuli placed at various locations around the centre of the receptive field. This could be inhibitory or excitatory in nature, and could be achieved by the weighting of lateral connections, as in the retina (Dacey, 2000).

Given the finding of a small number of V1 cells that were maximally responsive to aggregate feature types, questions emerge concerning the functional role of V1. If relatively complex feature based stimuli elicit preferential responses in V1 then it would suggest cells existed to support higher order roles in this area. This would be in line with studies that suggest the perceptual saliency and behavioural experience modulate cell response in V1 (Lee et al., 2002).

As previously detailed relatively small proportions of cells in V1 are found that show a pure chromatic response (i.e. a significant response to an equiluminant grating) (Johnson et al., 2001). In this thesis I used stimuli that contained both chromatic and achromatic modulation, as these approximate the type of stimuli that are found in the natural environment. For single ellipse stimuli, very few cells were found that showed a significant response. The behavioural results (Chapter 4 - Chapter 6) showed that the removal of the chromatic information impaired visual object recognition. Based upon these findings, questions emerged concerning why so few cells in marmoset V1 show chromatically based responses.

One possibility is that the effect that chromatic information has upon the visual process is manifested at a higher level (for example V2 or V4). Such theories have a degree of empirical support (Zeki, 1983b, Xiao et al., 2003), however a large body of work using various methodologies also exists supporting the role of V1 in chromatic processing (Engel et al., 1997, Lennie et al., 1990). The likely outcome is that stimulus chromaticity is expressed at a number of levels (Tootell et al., 2003) and the small number of chromatically selective cells found in my survey was due to the small sample size.

Despite the generally small numbers of chromatically responsive cells found in marmoset V1 I am proposing that the sensory contribution that colour makes is expressed at this level. Several factors point towards this. Firstly the feature like properties of the spatial selectivity of V1 cells seem suited to the representation of the visual scene. Although a small number of these cells were found that were significantly responsive to stimuli containing chromatic and achromatic modulation, it is in the interest of the visual process for cells to represent as wider range of stimulus dimensions at as fundamental level as possible. Lennie and colleagues describe V1 cells as exhibiting a multidimensional representation of the visual scene at the level of V1 and this remains an efficient and likely model of neural function (Lennie, 1998).

Secondly, previous studies in the marmoset have shown that the V1 cell response to achromatic gratings can be influenced or modulated by the superposition of a chromatic grating (Derrington et al., 2002). Here marmoset V1 cells are showing a clear effect based upon the presence of stimulus chromaticity. Although these effects tend to be reasonably subtle, they show that the chromatic properties of the visual scene

influence the way in which cells in V1 respond, and it seems logical that this effect leads to an important stage in the visual process, where by the comparative advantages relating to the luminance cues and chromatic cues are combined.

A degree of chromatic selectivity was also observed in a small proportion of the surveyed cells. Cells would therefore respond to yellow and not blue or blue and not yellow shifts in chromaticity. These results fit into traditional models of chromatic processing in V1 (De Valois and De Valois, 1993). The two chromatically opponent streams project to the level of V1, at which point theories suggest that cell response undergoes a stage of half wave rectification, to separate out the two chromatically opponent poles. Theoretical and physiological accounts of how neurons could perform this operation have been well documented.

The increasing chromatic selectivity present in V1 is of functional benefit for several reasons. By separating out the cardinal directions of colour space the cortical apparatus can represent a wider variety of colours and this is of obvious behavioural relevance. This is backed up by acute studies of macaque V1 that show neurons tuned to multiple directions of colour space across a broad range of the spectrum (Friedman et al., 2003). Similar results have been reported through the use of optical imaging techniques in V2 (Xiao et al., 2003). Such a transformation (between the LGN and V1) is of potential use in the development of the behaviourally relevant colour categories.

I therefore propose that the chromatic and achromatic properties of the visual scene remain segregated up to the level of V1 (as found by several previous studies: (Derrington et al., 1984, Chatterjee and Callaway, 2003)). Such segregation is required so that visual information can be encoded as efficiently as possible, this is required to

keep the size of the optic nerve to a minimum. At the level of V1, chromatic and achromatic information converge, in order to produce a representation of the visual image that is as behaviourally useful as possible. The achromatic pathway forms the basis of the representation, however this is influenced by the chromatic pathway, when stimulus colour is removed, the visual system is impeded as the combination of chromatic and achromatic information is behaviourally relevant.

9.6 FUTURE RESEARCH

The results of this thesis produce several further questions relating to the function of colour in human and non-human primate vision. These can be summarised by the following main points:

1) Is any advantage that is conveyed by colour, specific to the structural makeup of the objects? Does the selective finding of deficits in chromatic ability extend to objects of variable size and complexity?

2) Do the selective deficits in recognition memory relating to the subtraction of red-green information but not blue-yellow information extend to different classes of stimulus such as scenes or pictorial objects?

3) Do macaque monkeys provide similar deficits in object recognition based upon chromatic subtraction when tested on a serial recognition task opposed to list learning tasks?

4) Do trichromatic marmosets show a similar selective deficit to macaques when tested with objects that limit chromatic information to one or other of the opponent pathways?

5) Are any effects of chromatic or selective chromatic subtraction unique to a specific part of visual space? Are objects presented outside of fixation processed in a similar way to objects presented at fixation?

6) In trichromatic species, is the neuronal process in V1 relating to the combined processing of shape and colour biased towards one or the other of the opponent pathways?

7) Does feedback from higher visual areas (based upon the chromatic content of an image) affect the way in which V1 cells process chromatic information?

By characterising the interaction between stimulus structure and stimulus chromaticity it is possible to further develop theories relating to chromatic processing. Given that all of the effects observed within this thesis were based upon the removal of chromatic information that was presented within an underlying object based structure, it would be of interest to examine if effects of chromatic reduction were dependent upon structure. Does colour advantage recognition to a greater or lesser extent when objects become increasingly complex? Are effects modulated by the size or spatial frequency characteristics of stimuli?

Further studies could also examine whether the selective deficit unique to the red-green chromatic pathway in trichromatic subjects extends to other stimulus types. Work has already established that the removal of colour from natural scenes impedes recognition ability (Wichmann et al., 2002), however further study could examine whether this was specific to the removal of chromatic information relating to one or the other of the opponent pathways.

Future work could also examine whether stimulus chromaticity contributed towards vision differentially dependent upon the part of visual space that objects were situated in. A large body of research suggests that human colour vision is best when targets are presented fovealy. Work has already shown that chromatic sensitivity falls of with eccentricity (Mullen and Kingdom, 2002), and it would be of theoretical interest to examine whether such a fall off was also apparent in recognition abilities and whether or not this was similar for stimuli comprising of red-green or blue-yellow chromatic modulation.

Another area where the results of this thesis could be furthered is the methods that I used for the behavioural tests that used non-human primates. I used a list-learning paradigm as this represented an efficient way of testing visual object recognition abilities in the aforementioned species. One of the failings of this paradigm is that it does not allow measurement of ability over differential delay periods. This was one of the strengths of the studies with human subjects, which utilised a serial recognition paradigm. Future studies that taught macaques to respond to this type of continuous paradigm would be beneficial in confirming the deficits in ability that were observed in macaques were sensory in nature,

One of the unexpected findings in this thesis was that in human subjects, the subtraction of chromatic information carried by the primordial s-cone pathway had no effect upon object recognition ability. In dichromatic marmosets, who use this pathway to convey all chromatic information, the removal of stimulus chromaticity caused a deficit in recognition ability. I argued that the s-cone chromatically opponent pathway provided a differential contribution within each of the species.

Further insight could be gained by comparing the behavioural ability of trichromatic and dichromatic marmosets using similar techniques outlined within this thesis. Work has been carried out within this domain, however it has concentrated upon foraging ability, rather than the sensory aspects of visual recognition. If trichromatic marmosets also showed a deficit in recognition ability by the reduction of s-cone pathway specific chromaticity then it would further the conclusions that relate to species differences.

Further work addressing the functional differences between the red-green and blue-yellow opponent pathways could also examine the contribution of neuronal response at various levels along the visual pathway. As the S-cone pathway predates the more recently evolved red-green pathway and has been shown to project along a morphologically separate pathway it remains a possibility that anatomical areas higher up the visual pathway may also reflect this difference. Work in V2 has already shown that adjacent areas in cortex show organisational principles relating to the representation of the stimulus hue (Xiao et al., 2003), and a possibility remains that as visual information projects to higher anatomical areas, there is a bias towards certain regions (such as red) within the chromatic spectrum. By combining more refined cell recording and cortical inactivation techniques it will be possible to assess the function of cortical areas along the ventral visual stream and the degree to which chromatic information and specific chromatic information interacts with these areas. Further investigation into the representation of visual structure by the ventral visual stream is also required if theories of chromatic processing and the representation of visual structure are to be combined.

Therefore the finding of a small number of feature driven cells in marmoset V1 is a definite prompt for further research. Studies that have examined the spatial selectivity of cells in V1 have used a gabour patch model originally defined from the reverse correlation techniques (Jones and Palmer, 1987b). As detailed in the introduction, results were generally convergent upon the original empirical findings of Hubel and Wiesel (Hubel and Wiesel, 1962). More recently modelling studies have suggested that the visual process can benefit from an over-complete representation of the visual world (Riesenhuber and Poggio, 2000). Based upon these hierarchical feed-forward models of visual function, the most efficient way of representing the visual world is to use multiple spatial filters that are similar in nature and represent the fundamental units of the visual scene (e.g. lines and intersections).

In order for the visual process to be as efficient in the way it utilises spatial filtering to represent the visual world, I suggest that higher order feature based spatial filters would also be beneficial, at a reasonably early stage in the visual process. Such filters allow a sparse representation of the visual scene to be established. Further studies using more effective receptive field mapping techniques, at a finer resolution afforded by the sinusoidal grating would be beneficial in validating this argument.

9.7 FINAL CONCLUSION

In conclusion, colour makes a contribution to the visual object recognition for humans, macaques and marmosets. This was evident from the fact that when colour was removed from non-nameable object stimuli, recognition ability was impeded. This finding informs the debate relating to the function of colour, in as much as it shows that colour contributes at a sensory level as well as a higher cognitive level.

Of further functional relevance is the difference that was observed between effects of removing chromatic information that was conveyed by the red-green pathway compared to the blue-yellow pathway. For humans, the removal of red-green chromatic modulation leads to a deficit in recognition ability where as the removal of blue-yellow information did not. I conclude that for human, the advantage that chromatic information provides is biased towards red-green information.

Such a hypothesis is compatible with evolutionary accounts that red-green chromatic opponency evolved specifically for the purpose of detecting fruit from foliage, and would therefore be advantageous in the recognition of natural objects. However the results with dichromatic marmosets show that the primordial s-cone system still provides an advantage in object recognition and so any deficits in ability caused by chromatic subtraction are not unique to one of the opponent pathways when comparisons are made across species.

I therefore conclude that the visual system is liable to show bias dependent upon the type and range of chromatic information available to it. In the case of dichromatic animals, the visual system has no option but to utilise the chromatic information provided by the s cone pathway, and so a corresponding deficit is observed when chromatic information is removed from stimuli. In the case of trichromatic animals, the visual system is biased towards the red-green opponent system as it is superior in nature, and therefore shows a selective deficit when information relating to the alternative pathways is removed.

Given that I observed a bias in ability relating to the presence of red-green chromatic information, at what point does this arise in the visual pathway? Although I

carried out no tests on the neuronal response in trichromatic animals, the discovery of cells that show a modulation in response to achromatic gratings, based upon the addition of chromatic information would provide a candidate substrate for the process of combining chromatic and achromatic cues. These cells have been shown in marmoset V1 and V2 (Derrington et al., 2002) and could be advantageous in the development of feature like units that show balance the chromatic and achromatic properties of objects.

Based upon the fact that the opponent pathways project up to the level of V1, I suggest that lateral connectivity within V1 combines cell responses to multiple stimulus attributes to produce higher order representations that combine selectivity for colour and luminance. This type of process was apparent by the discovery of the hyper complex feature detecting units within the area.

At the point where the chromatic and achromatic channels are combined, I suggest that the increased resolution and lack of chromatic aberration relating to the red-green pathway makes it preferable in the development of an abstract representation of the visual scene. Further research is required to extend and elaborate upon these ideas, however they would explain many of the studies that show increased recognition / discrimination abilities relating to the specific red or green hues.

Such a model does not account for the feedback connection from higher visual areas and is somewhat underspecified. However, I hope that further work combining behavioural and physiological measures can further elaborate upon the type of neuronal processes that are allowing humans and non human primates to exploit the chromatic properties of the visual scene in recognition behaviour. As methods and techniques advance more accurate and wider ranging theories of the relationship between cell firing

and visual perception will emerge, A great deal of progress has been made within the past 50 years, and a framework is beginning to emerge relating to how the brain processes information. Such a framework is critical to the advancement of scientific theory within this discipline and beyond.

9.8 REFERENCES

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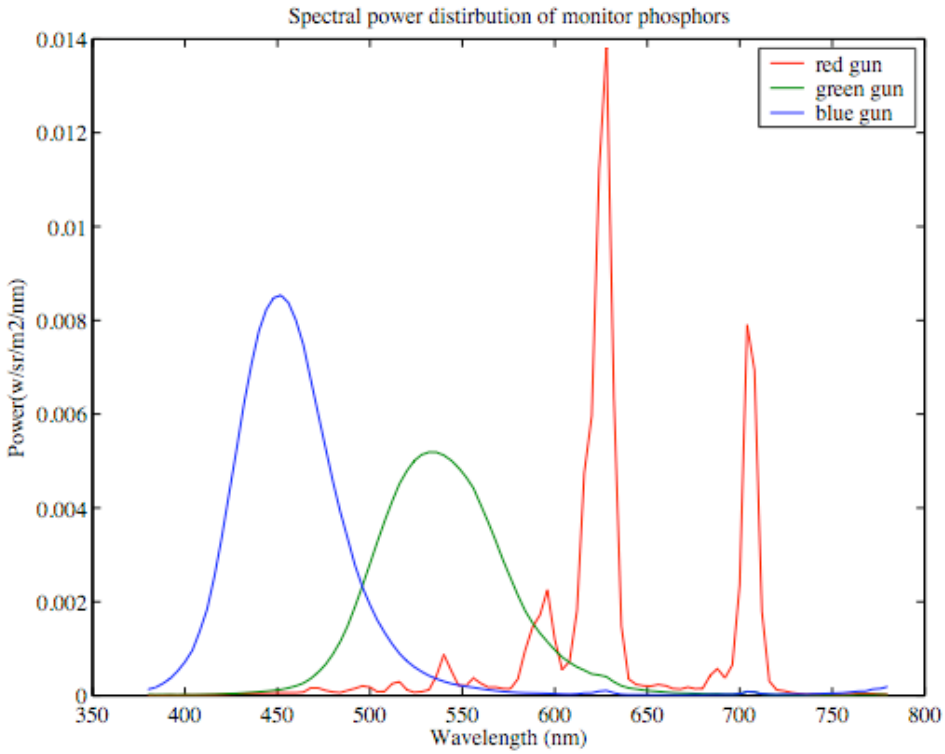
Chapter 10 APPENDICES

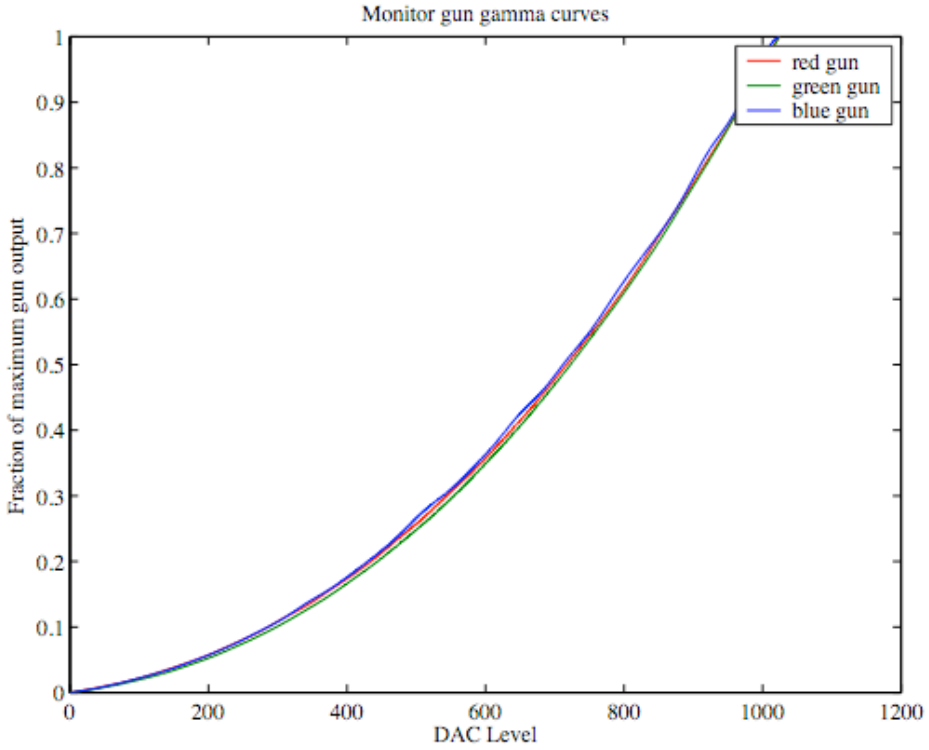
10.1 SCREEN CALIBRATION

10.1.1 Serial recognition rig

10.1.1.1 Serial recognition rig phosphor output



10.1.1.2 Serial recognition rig luminance output

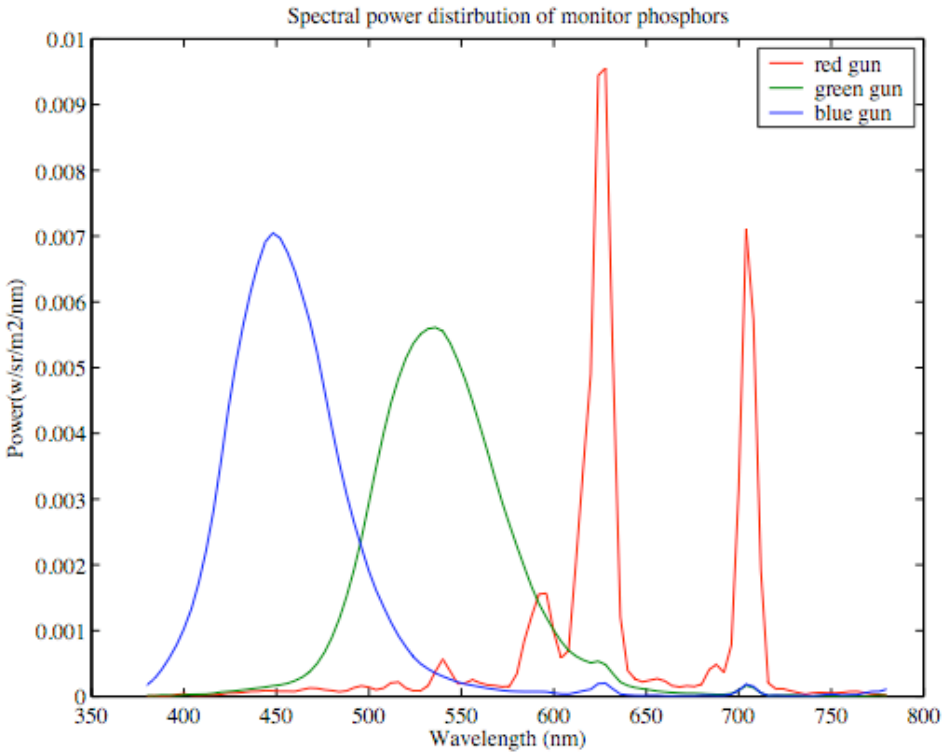


10.1.1.3 Serial recognition calibration accuracy

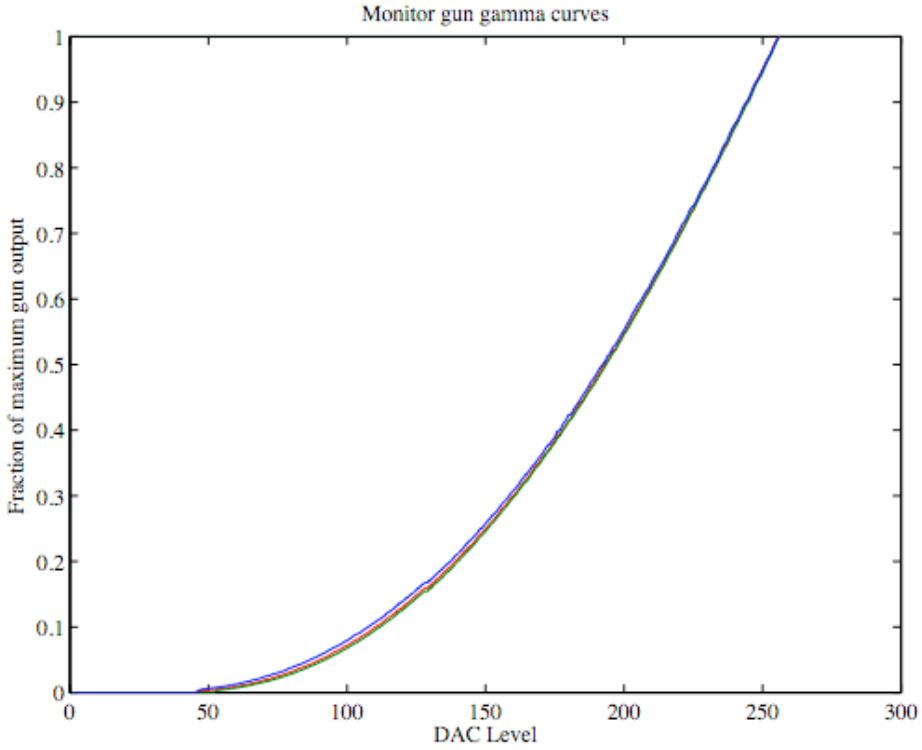
	X	Y	Y	G_0	γ	RMS Error
Red	0.6098	0.3463	18.2312	0	1.5778	0.9985
Green	0.2982	0.5997	55.4021	0	1.6051	0.9985
Blue	0.1499	0.0728	10.7736	0	1.5543	0.9985

10.1.2 Touch screen rig

10.1.2.1 Touch screen rig phosphor output



10.1.2.2 Touch screen rig luminance output

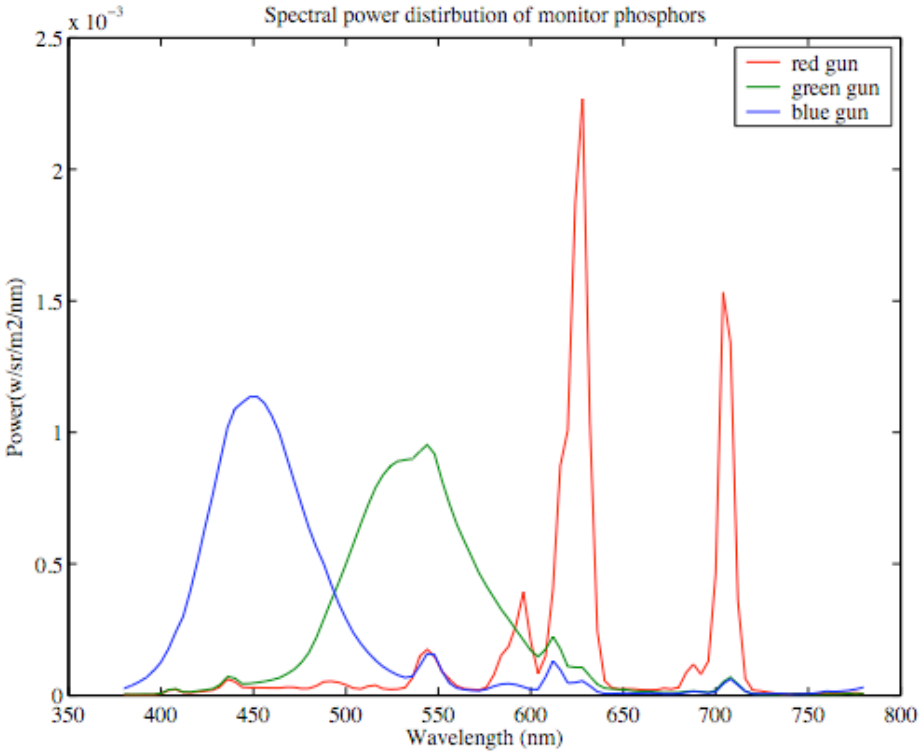


10.1.2.3 Touch screen rig calibration accuracy

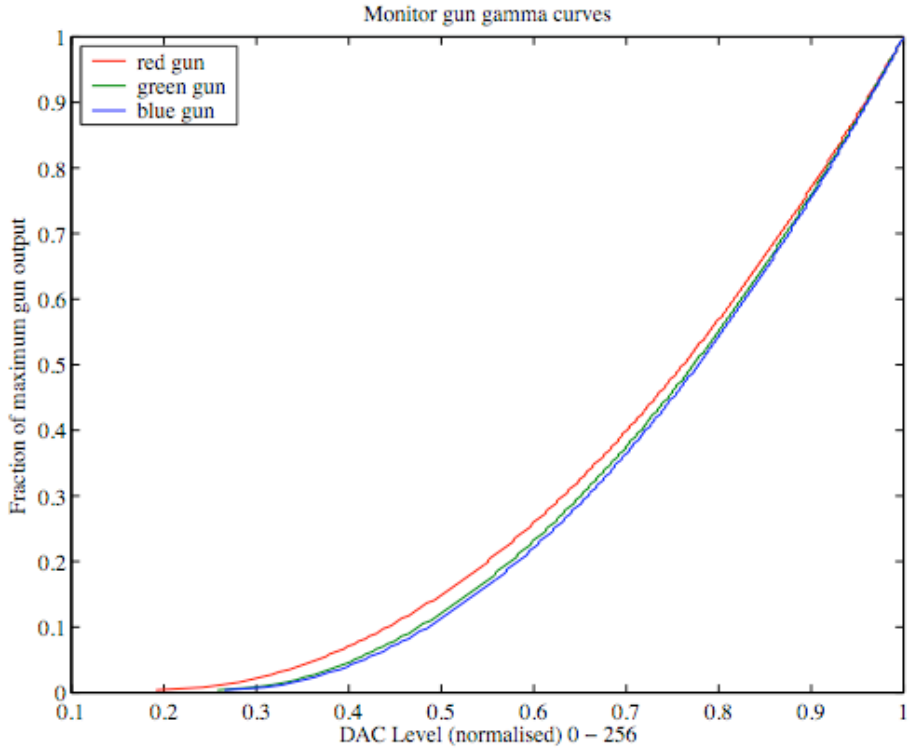
	x	Y	Y	G_0	γ	RMS Error
Red	0.6089	0.3491	14.9473	0	1.8893	0.9943
Green	0.2978	0.6032	58.3656	0	1.9038	0.9944
Blue	0.1524	0.0800	10.2627	0	1.8637	0.9943

10.1.3 Y Maze rig

10.1.3.1 Y Maze rig phosphor output



10.1.3.2 Y Maze rig luminance output

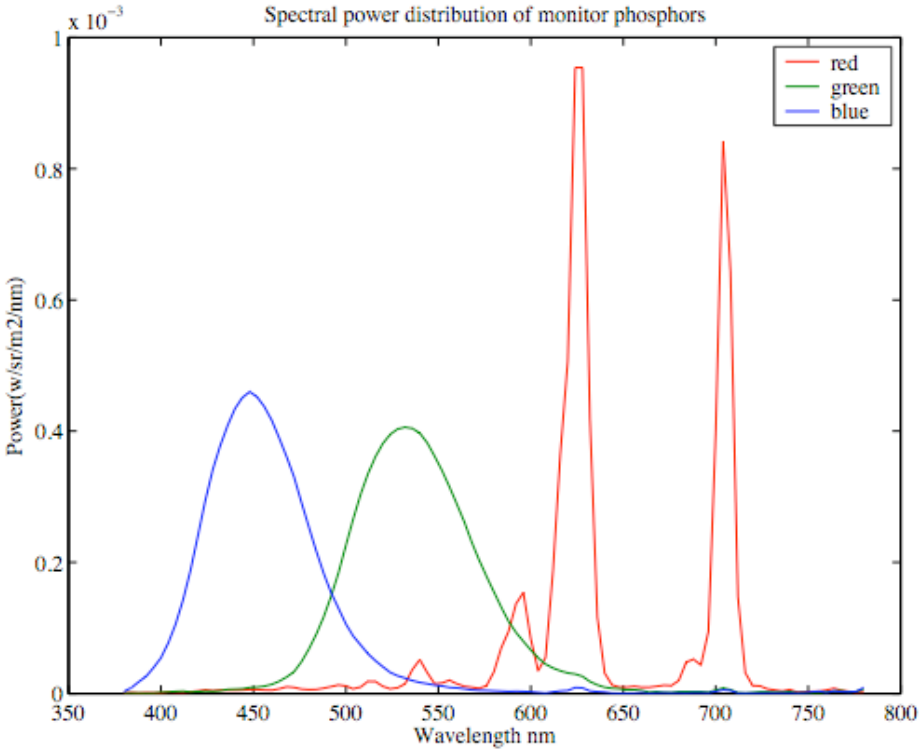


10.1.3.3 Y Maze rig calibration accuracy

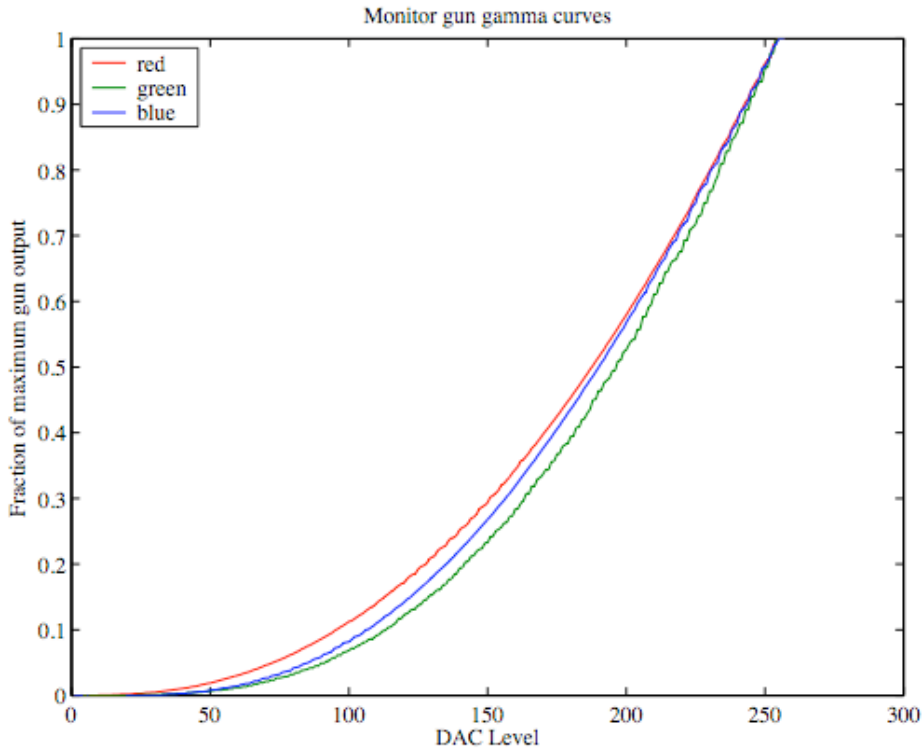
	x	y	Y	G_0	γ	RMS Error
Red	0.4008	0.3288	6.7154	0	2.2738	0.994
Green	0.2956	0.4481	11.3221	0	2.4494	0.994
Blue	0.2225	0.1965	5.6128	0	2.5097	0.994

10.1.4 Neurophysiology rig

10.1.4.1 Neurophysiology rig phosphor output



10.1.4.2 Neurophysiology rig luminance output



10.1.4.3 Neurophysiology rig calibration accuracy

	x	Y	Y	G_0	γ	RMS Error
Red	0.6247	0.3447	5.307	0	1.7290	0.994
Green	0.2886	0.6133	16.47	0	1.9159	0.994
Blue	0.1495	0.0697	2.269	0	1.8023	0.994

10.2 FLOWER-LIKE OBJECT MATLAB CODE

10.2.1 Main stimulus generation program

```
% Blobject generation program
% Makes a blobject matrix and / or plots it
% Requires three files:
%
% The equipment file contains information regarding the
% current environemnt
%
% The parametrs files contains information regarding the
% current type of blobject.
```

```
%
% Takes the following parameters:
%
% Equipment - name of equipment MATLAB variable
% Parameters - name of parameters file
% PlotF -   flag to specify whether the program plots the blobject
%                 on screen: 1= plot 0 = dont plot
% ReturnF - flag to specify whther the programs returns a blobject
%                 matrix: 1=return blobject matrix 0 = dont return
blobject
%                 matrix
% GenerateF - flag to specify whether the program generates blobject
parameters
%                 or plots them from a matrix. 1= generate, 0= take
blobject matrix
% bObject - a blobject matrix of the type returned by the program used
if you dont
%                 generate.
%
%                 You can't return params if you choose not to generate
them...
%                 You can't plot params if you dont generate or supply
them
%                                     P R G
%                 Thus you can 1 1 1
%                                     1 0 0 - if you supply a blobject
matrix
%                                     1 0 1
%
% Returns the following parameters:
% Blobject - a cell array of the blobject parameters


function [out] =
BProg(equipment,parameters,clut,plotF,returnF,generateF,bobject)


% Declare local variables


fid = 99;          % Varibale for file identification
strVal = '';       % Variable for reading in data
i = 1;                   % Counting variable
nEllipses = 0;
```

```
% Read in infomation from file

fid = fopen(parameters,'rt');

while feof(fid) == 0
      strVal = fgets(fid);
      if strVal(1) ~= '%'
            strVal = str2num(strVal);
            blobParameters(i) = strVal;
            i = i+1;
      end
end

fclose(fid);



% Set random number generator

rand('state',sum(100*clock));

% Set blobject variables

% Constant statics params

steps = 50;
t = [pi/steps:pi/steps:2*pi];
dtr = pi/180;
rot = 90;
rotr = rot*dtr;

if generateF == 1

      % Static params

      plotSize = blobParameters(1);
```

```
	backGround = blobParameters(2);
	centreX = blobParameters(5);
	centreY = blobParameters(6);
	ellipseToAR = blobParameters(7);
	minEllipse = blobParameters(8);
	startOr = blobParameters(9);

	% Distribution params

	petalSize = [blobParameters(10) blobParameters(11)
blobParameters(12) blobParameters(13)];
	orAdd = [blobParameters(14) blobParameters(15) blobParameters(16)
blobParameters(17)];
	baseAR = [blobParameters(18) blobParameters(19)
blobParameters(20) blobParameters(21)];
	ARAdd = [blobParameters(22) blobParameters(23) blobParameters(24)
blobParameters(25)];
	cSize = [blobParameters(26) blobParameters(27) blobParameters(28)
blobParameters(29)];
	cAR = [blobParameters(30) blobParameters(31) blobParameters(32)
blobParameters(33)];


	% Clut variables

	clutSize = blobParameters(34);
	clutZoneSize = blobParameters(35);
	clutOffset = blobParameters(36);
	clutZone = blobParameters(37);

end

% Calculated variables

if generateF == 1

	petalSize = randnorm(petalSize);

	while nEllipses < minEllipse
		baseAR = randnorm(baseAR);
		nEllipses = baseAR*ellipseToAR;
```

```
      end



      nEllipses = ceil(nEllipses);


end

% Create blobject object matrix

if returnF == 1

      bobject = cell(nEllipses,11);

      bobject(1,1) = {plotSize};
      bobject(1,2) = {backGround};
      bobject(1,3) = {centreX};
      bobject(1,4) = {centreY};
      bobject(1,5) = {rand('state')};
      bobject(1,6) = {petalSize};
      bobject(1,7) = {nEllipses};
      bobject(1,8) = {baseAR};

end

% Read from object matrix if flaged

if generateF ~= 1

      plotSize = bobject{1,1};
      backGround = bobject{1,2};
      centreX = bobject{1,3};
      centreY = bobject{1,4};
      petalSize = bobject{1,6};
      nEllipses = bobject{1,7};
      baseAR = bobject{1,8};
```

```
end



% Start plotting blobject - put up background

if plotF == 1

      close all;
      fg1 = figure;
      theMap = clut;
colormap(clut);

      set(fg1,'Visible','on');
      set(fg1,'BackingStore','off');
      plotsize = 175;
      p1 = patch([-plotsize/2 plotsize/2 plotsize/2 -plotsize/2],[-
plotsize/2 -plotsize/2 plotsize/2 plotsize/2],2);
      set(p1,'CDataMapping','direct')
      set(p1,'LineStyle','none');
      set(gca,'Visible','off');

      axis([-plotsize/2 plotsize/2 -plotsize/2 plotsize/2]);hold on;
      %set(gcf,'Position', [256 334 412 284])



end

% Plot blobject

for i = 1:nEllipses

      % Set petal colour

      if generateF == 1

            rgb = ceil(rand(1) * clutZoneSize);
            rgb = rgb+clutOffset*clutZone;
```

```
end

% Record petal colour in object matrix

if returnF == 1

      bobject(i,9) = {rgb};

end

% Read from object matrix if needs be

if generateF ~= 1

      rgb = bobject{i,9};

end

% Vary aspect ratio


if generateF == 1

      AR = baseAR+randnorm(ARAdd);

end

% Read from object amtrix if needs be



% Record aspect ratio in object matrix

if returnF == 1

      bobject(i,10) = {AR};

end
```

```
if generateF ~= 1

      AR = bobject{i,10};
end

% Work out increase in or

if generateF == 1

      rotAdd = randnorm(orAdd);

end

% Record increase in or in object matrix;

if returnF == 1

      bobject(i,11) = {rotAdd};

end

if generateF ~= 1

      rotAdd = bobject{i,11};

end

      % get rid of first centering segment by blending it into the
background

      if i == 1
            if generateF == 1
                  rgb = backGround;
            end

            if returnF == 1
                  bobject(i,9) = {rgb};
            end
```

```
      if generateF ~= 1
            rgb = bobject{i,9};
      end
end




% Create center if needs be

if i == nEllipses

            if generateF == 1

                  AR = randnorm(cAR);
                  petalSize = randnorm(cSize);



                  rgb = ceil(rand(1) * clutZoneSize);

                  rgb = rgb +clutZone*clutOffset;

                  centreX = 0;
                  centreY = 0;
            end


      % Record center prams in object matrix

      if returnF == 1

            bobject(i,10) = {AR};
            bobject(i,6) = {petalSize};
            bobject(i,9) = {rgb};
            bobject(i,3) = {centreX};
            bobject(i,4) = {centreY};
```

```
      end

      if generateF ~= 1

            AR = bobject{i,10};
            petalSize = bobject{i,6};
            rgb = bobject{i,9};
            centreX = bobject{i,3};
            centreY = bobject{i,4};

      end

      end


% Plot ellipse

cosrot = cos(rotr) * petalSize;
sinrot = sin(rotr) * petalSize;
b = 1/sqrt(AR);
a = 1/b;
x = a * cos(t) ;
y = b * sin(t) ;
rotx = x * cosrot - y * sinrot + centreX;
roty = y * cosrot + x * sinrot + centreY;
rot = rot+rotAdd;
rotr = rot*dtr;
centreY = sin(rotr)*(0.5*petalSize*AR);
centreX = cos(rotr)*(0.5*petalSize*AR);

if plotF == 1
      p = patch(rotx,roty,rgb);
      % set(p0, 'EdgeColor',colormap(rgb,:));
      set(p,'CDataMapping','direct');
      set(p,'LineStyle','none');
end
```

```
end

if plotF == 1

      axis off;

end

if returnF == 1

      out = bobject;

end
```