A PSYCHOPHYSICAL INVESTIGATION OF HUMAN VISUAL PERCEPTUAL MEMORY

A study of the retention of colour, spatial frequency and motion visual information by human visual short term memory mechanisms

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to my Parents

Abstract

A Psychophysical Investigation of Human Visual Perceptual Memory

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The aim of this thesis was to investigate how visual information is organised in perceptual short term memory, with special interest in colour, spatial frequency and velocity. Previous studies of VSTM have indicated the existence of specific memory mechanisms for visual attributes such as orientation, spatial frequency, velocity, contrast and colour. The retention of information in visual short term memory for these basic visual attributes can be disrupted by the presentation of masking stimuli during inter-stimulus intervals (ISIs), which are outside the range of traditional sensory masking. We exploited this memory masking effect in order to examine the organisation of visual information in VSTM. Four groups of experiments were conducted in which participants carried out a delayed discrimination paradigm that employed a two-alternative forced choice (2-AFC) procedure in conjunction with a method of constant stimuli. The fidelity of VSTM was measured by performance markers such as discrimination thresholds and point of subjective equalities. We have found selective memory masking effects, which serve as further evidence in favour of the modular organisation in VSTM, namely, that human visual perceptual memory is based upon multiple, tuned channels in case of colour, spatial frequency and speed, similar to those found in the earliest stages of visual processing for spatial frequency. Moreover, each of these storage mechanisms are tuned to a relatively narrow range of stimulus parameters that are closely linked to visual discrimination mechanisms. These findings add further support to the view that low-level sensory processing mechanisms form the basis for the retention of colour, spatial frequency and velocity information in perceptual memory. We also found evidence for the broad range of transfer of memory masking effects across spatial location, which indicates more long range, long duration interactions between channels that are likely to rely upon contributions from neural processes located in higher visual areas. In conclusion, the experiments presented in this thesis provide significant insight into the organization of visual information in perceptual short term memory.

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Chapter 1

Introduction to Vision

1.1 Colour Vision

In this section I will review the basic anatomy and physiology of colour vision. Colour vision is the ability of the visual system to distinguish objects based on the analysis of the energy and wavelengths of the light that reaches the eye. Colour vision facilitates the discrimination and faster recognition of objects in the environment and enables the formation of precise memory representations (Gegenfurtner & Rieger, 2000).

1.1.1 The Retina

1.1.1.1 Photoreceptors

Light that reaches the eye is absorbed by rod and cone photoreceptors. Three classes of cones serve as the basis for trichromatic vision. All cones get activated by a wide range of wavelengths, and are named short (S), middle (M), and long (L) wavelength sensitive cones, based on their peak sensitivity. L cones have their peak sensitivity at approximately 560 nm (red), M cones at 530 nm (green) and S cones at 430 nm (blue) (Smith & Pokorny, 1975; Solomon &

Lennie, 2007; Stockman & Sharpe, 2000) (**Figure 1.1**). The absorption spectra of the M and L cones overlap to a great extent, which on one hand might impair colour vision but on the other hand leads to a higher achievable spatial acuity in the fovea, since the visual system ignores the small difference in the absorption spectra when it extracts information for spatial vision (Gegenfurtner & Kiper, 2003). Cones in the retina are organized in a single layer in an uneven, random spatial arrangement (Curcio et al., 1991; Mollon & Bowmaker, 1992). The ratio of M and L cones shows a high degree of variation across individuals (Curcio et al., 1991; Mollon & Bowmaker, 1992; Roorda & Williams, 1999; Wassle & Boycott, 1991), but overall the relative number of L cones compared to M cones shows a gradual increase towards the periphery (Murray et al., 2006). S cones constitute approximately 10-18% of the total cone photoreceptor population (Wassle & Boycott, 1991), they are absent in the foveola (central 100 microns/0.35°), reach their maximum density at 2° of retinal eccentricity and gradually decrease towards the periphery (Curcio et al., 1991).

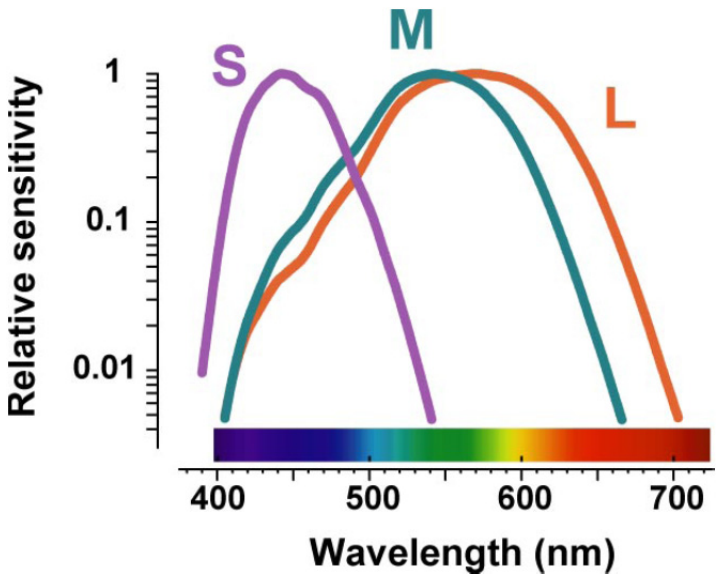


Figure 1.1 The relative spectral sensitivities of the S-, M- and L cones based on the cone sensitivity measurements of Stockman & Sharpe (Stockman & Sharpe, 2000). Even though the peak sensitivities differ, the sensitivity spectrums show a great amount of overlap. (Source: (Gegenfurtner & Kiper, 2003)).

The chance of a photon being absorbed by the photoreceptors depends on its wavelength, but once it is absorbed it is processed as an electrical signal, which represents the number of photons that were absorbed by each photoreceptor, independent of the original wavelength. This is known as the Principle of Univariance (Rushton, 1972). Wavelength discrimination is facilitated in the chromatic postreceptoral pathways, at the level of the horizontal and ganglion cells, by comparing the activation of the different types of photoreceptors.

According to the trichromatic theory of colour vision (Helmholtz, 1852; Young, 1974) colour vision is based on the activation of three distinct mechanisms, depending on the wavelength of the absorbed light that are related to the three primary colours. The trichromatic theory of colour vision failed to describe all aspects of colour vision such as chromatic afterimages and the absence of certain colour combinations. Based upon the perceptual experience of colours, Hering developed the opponent colour processing theory (Hering, 1964). After long debate it has been widely accepted that chromatic processing at the level of the cones is explained by the trichromatic theory, whereas the opponent processing theory describes chromatic processing at, and beyond the level of the ganglion cell layer. According to the opponent theory, colour information is processed via two different channels, L-M (‘red-green’) and S-(L+M) (‘blue-yellow’). The opposing L and M inputs form the so called ‘red-green’ channel and the comparison of S cone inputs with the sum of L and M cone signals form the so called ‘blue-yellow’ channel. The third, luminance channel is created by the sum of the inputs from L and M (L+M) cones (**Figure 1.2**).

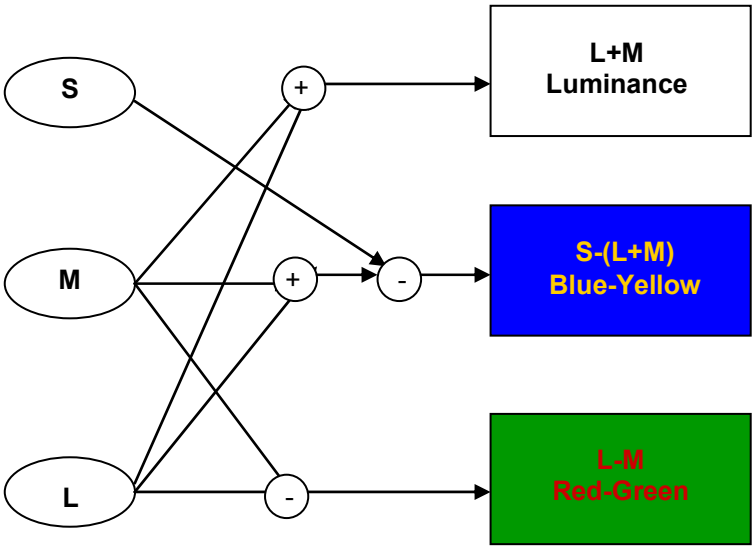


Figure 1.2 Cone opponent pathways between the retina and the LGN. The retinal signals from the cones are combined in three different ways in order to carry colour and luminance signals (De Valois & De Valois, 1993; De Valois et al., 1966b; Derrington et al., 1984; Krauskopf et al., 1982).

These three post-receptoral pathways transmit signals from the cones to the cortex (Krauskopf et al., 1982). According to electrophysiological studies these separate processing channels form anatomically and physiologically distinct pathways, and terminate in different layers of the Lateral Geniculate Nucleus (LGN) and Visual Cortex (De Valois et al., 1966a; De Valois & De Valois, 1993). L-M information is transmitted via the parvocellular-, and +S-(L+M) information via the koniocellular pathway (Hendry & Yoshioka, 1994). Luminance (L+M) information is conveyed via the magnocellular pathway (Derrington & Lennie, 1984).

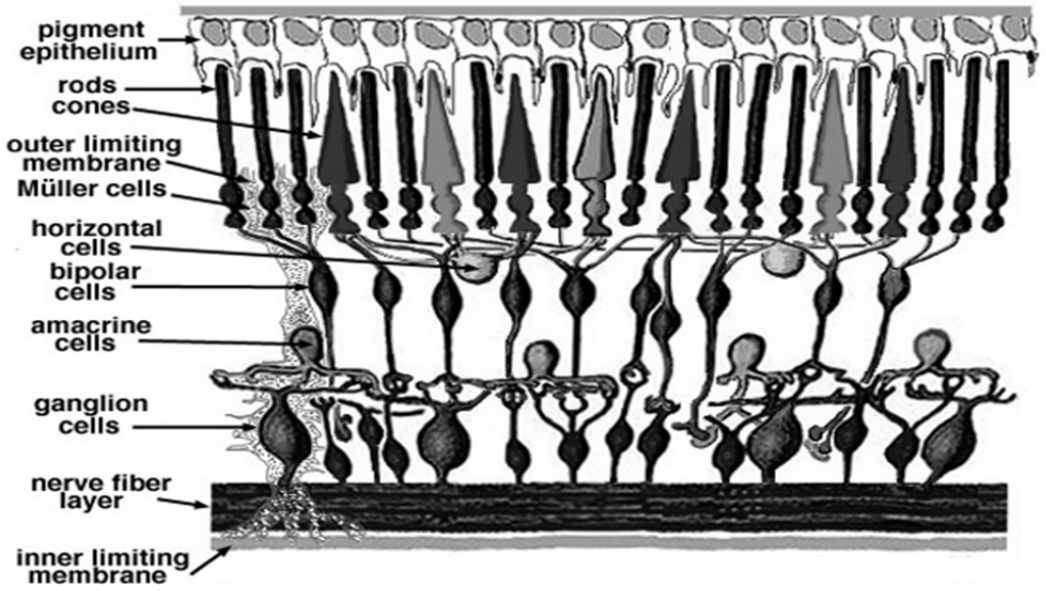


Figure 1.3 Cellular organization of the human retina, indicating the different cell types as well as their location in the retinal layers. Receptors (cones and rods) make specific contact with various bipolar and horizontal cell types. In the inner retina, the bipolar cells convey signals to the main ganglion cell types.
(Kolb, H. (n.d.) [Online Image] Available at: <http://webvision.med.utah.edu/book/part-i-foundations/simple-anatomy-of-the-retina/> [Accessed 14 July 2010]).

1.1.1.2 Horizontal Cells

Horizontal cell bodies are found in the Inner Nuclear Layer (INL) of the retina, their dendritic processes connect with photoreceptors and their axons connect with bipolar cells (**Figure 1.3**) (Dacey, 1999; Wassle & Boycott, 1991). Each horizontal cell is connected with 15-25 cones in the fovea, and the number of connections gradually decreases to 10-15 in the periphery (Wassle & Boycott, 1991; Wassle et al., 1989). There is no colour specific response at the level of horizontal cells, since they non-selectively connect with all types of cones (Wassle & Boycott, 1991) and transmit all cone signals to bipolar cells by hyperpolarization, without reference to the wavelength of the absorbed light. They provide negative feedback to the photoreceptors facilitating lateral inhibition and they are believed to contribute to the generation of antagonistic receptive field surrounds of bipolar and ganglion cells, by feedback or feed-

forward mechanisms (Dacey, 1999; Dacey et al., 1996; Wassle & Boycott, 1991). Depending on their morphology and connection preferences with the three cone types, there are two main categories of horizontal cell that have been identified so far (Wassle & Boycott, 1991; Wassle et al., 1989). H1 cells connect with M, L and randomly with some S cones. H2 cells on the other hand connect mainly with S cones and also with some L and M cones (Dacey, 1996; Wassle & Boycott, 1991). However, some studies identified an additional, third type of horizontal cell in humans, H3 which only connects to L and M cones selectively, and could provide evidence for the existence of possible colour selectivity at the level of horizontal cells (Ahnelt & Kolb, 1994).

1.1.1.3 Bipolar Cells

Bipolar cells transmit photoreceptor signals to the amacrine and ganglion cells via the horizontal cells (**Figure 1.3**). There are more than ten different types of bipolar cell identified in the retina (Boycott & Wassle, 1991; Kolb et al., 1992) and depending on their connections they can be classified into three main classes; midget, diffuse and S-cone selective (blue-cone bipolar) (Dacey, 1999; Kouyama & Marshak, 1992). They are also classified based on their activation patterns; light increments depolarise ON-bipolar cells whereas they hyperpolarize OFF-bipolar cells. It is still unclear whether, and how, bipolar cells contribute to colour opponency. Studies have shown that they have a centre surround receptive field organization (Dacey, 1999) and at this level 'red-green' cone opponency is formed by opposite signals from L and M cones into the receptive field centre and surround. For example, the centre of the receptive field receives ON input from M cones and the surround receives OFF input from L cones, therefore both centre and surround receive cone specific signals (Lee

et al., 1988; Martin et al., 2001). Bipolar cells specifically connect with the ON (ON-bipolar) or OFF (OFF-bipolar) receptive field centre of single ganglion cells and the surround always has the opposite signal input (Wassle & Boycott, 1991; Wiesel & Hubel, 1966).

1.1.1.3.1 Diffuse bipolar cells

Diffuse bipolars are further subdivided into ON and OFF bipolar subgroups (Boycott & Hopkins, 1991; De Valois & De Valois, 1993). They receive a summed input from neighbouring L and M cones to the centre and surround of the receptive field and show strong spectral sensitivity. A single diffuse bipolar cell non-selectively connects with several cones therefore it receives summed inputs from M and L cones into the centre and surround of their receptive fields (Boycott & Hopkins, 1991; Wassle & Boycott, 1991).

1.1.1.3.2 Midget bipolar cells

Midget bipolar cells receive opposing L and M cone inputs and have an antagonistic centre surround receptive field organization. Midget bipolar cells are 50% ON and 50% are OFF types (Boycott & Hopkins, 1991). Each cone connects with a single ON or OFF midget bipolar cell in a private line arrangement in the fovea which results in high spatial acuity (Boycott & Hopkins, 1991; Calkins & Sterling, 1999; Wassle & Boycott, 1991). In the periphery (beyond 50° eccentricity), 3-5 cones connect with a single midget bipolar cell (Dacey, 1999; Wassle et al., 1994).

1.1.1.3.3 S-cone bipolars

S-cone bipolars connect exclusively with short wavelength sensitive cones and depolarize as a result of S cone activation. Each S-cone bipolar connects to 1-2 S cones on average (Kouyama & Marshak, 1992) and the number of ON

responses outnumbers the OFF responses (De Valois & De Valois, 1993; Kouyama & Marshak, 1992).

1.1.1.4 Ganglion Cells

There are approximately one million ganglion cells in the retina. Their cell bodies are located in the ganglion cell layer, their axons in the nerve fibre layer and their dendrites extend into the inner plexiform layer (**Figure 1.3**) (Boycott & Wassle, 1974). The density of the ganglion cells is highest in the fovea and gradually decreases with increasing retinal eccentricity (Wassle et al., 1989). In the fovea more than three ganglion cells connect with one cone (Wassle et al., 1989) and there is a 1:1 cone specific connection between ganglion and bipolar cells. Ganglion cells in the central retina have small receptive fields that gradually increase towards the periphery (Dacey, 1993). There are three main types of ganglion cell, which have different morphological properties and central projections; parasol (P cells), midget (M cells) and small bistratified cells (Dacey & Lee, 1994; Leventhal et al., 1981; Perry & Cowey, 1984).

1.1.1.4.1 Parasol ganglion cells

The parasol ganglion cells have large cell bodies and dendritic trees, and project to the magnocellular layers of the LGN (M-pathway), where typically non-opponent type cell responses are registered (Perry & Cowey, 1984). Parasol cells are the anatomical equivalents of macaque M cells which are responsible for motion detection, luminance function, have high temporal frequency contrast sensitivity and low spatial frequency contrast sensitivity, and have low sensitivity to coloured stimuli (Lee et al., 1988). They have large ON/OFF centre receptive fields and receive summed inputs from L and M

cones. Each of these ganglion cells has extensive dendritic trees connecting with 20-25 cones through diffuse bipolars (De Valois & De Valois, 1993).

1.1.1.4.2 Midget ganglion cells

Midget ganglion cells transmit L-M opponent signals to the parvocellular layers of LGN via the P-pathway and they are very similar to macaque P-cells. They respond best to low temporal frequency and chromatic stimuli (Derrington et al., 1984). In the central 7-10°, each midget ganglion cell is connected with a single midget bipolar in a 'private line arrangement' through a number of synapses (Calkins et al., 1994; Kolb & Dekorver, 1991). In this region colour opponency is constructed automatically as they receive selective inputs from L or M cones to the centre of their receptive fields via a bipolar cell (Dacey, 1999). The surround either receives antagonistic input from L or M cones or from mixed cone types (Calkins et al., 1994; Wassle & Boycott, 1991; Wiesel & Hubel, 1966). Toward the periphery the size of the dendritic field increases and more bipolars are connected with each ganglion cell, therefore the 'private line arrangement' is no longer present (Dacey, 1999). Midget ganglion cells in the periphery receive signals from both M and L cones to the centre and surround of their receptive field (Dacey, 1999). There are conflicting views in the literature regarding the structure of retinal projections to the ganglion cell receptive fields in the periphery (**Figure 1.4**). According to the 'random wiring hypothesis', both the centre and surround of the receptive field randomly receive mixed inputs from cones (Dacey, 1996, 2000; Dacey & Packer, 2003). According to this, the quality of chromatic vision diminishes towards the periphery, due to a decrease in L/M cone opponency. However, studies in favour of this hypothesis do not account for the cortical magnification factor, namely, the progressively

increasing receptive field size towards the periphery. Other studies found that if a stimulus size is sufficiently increased in the periphery the colour discrimination ability remains as accurate as in the fovea (Abramov et al., 1991; Vakrou et al., 2005). This finding supports the 'cone selective hypothesis', which states that the selective connectivity is maintained in the periphery but it is reduced due to the decrease in the number of L and M cones, therefore the stimulus size has to be increased in order to account for this and maintain colour discrimination ability in the periphery (Lee et al., 1998; Reid & Shapley, 2002; Vakrou et al., 2005).

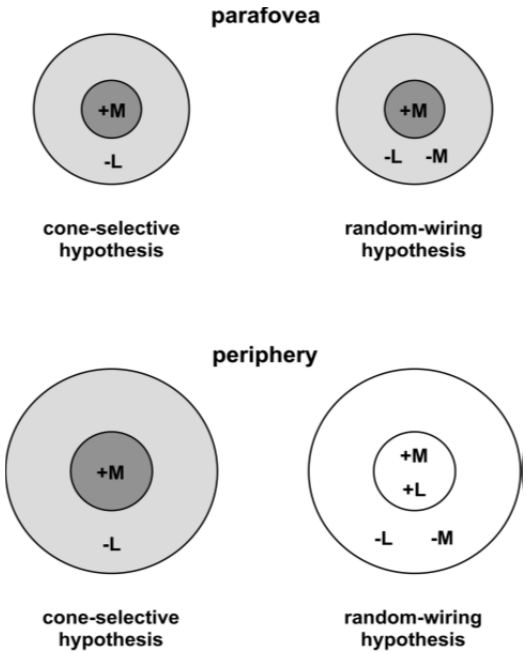


Figure 1.4 Cone opponency in the midget ganglion cells in the parafoveal and peripheral retina. Models for L/M chromatic opponency are based on antagonistic cone inputs to the centre and the surround of the receptive field. According to the cone selective hypothesis, in the parafoveal region, a single cone (+M) provides input to the receptive field centre of the ganglion cell, and the surround receives an opposing signal from a different cone type, or, according to the random wiring hypothesis, from a mixture of cones. In the periphery, the ganglion cells have much larger receptive fields but chromatic opponency is still preserved according to the cone-selective hypothesis. However, the random-wiring hypothesis suggests that both the centre and the surround of the cell receive mixed inputs therefore cone-opponency disappears (Source: (Vakrou et al., 2005)).

1.1.1.4.3 Small bistratified ganglion cells

These cells were identified by Dacey through intracellular staining of macaque retina (Dacey, 1993). They receive excitatory S cone (S-ON cell) (Dacey & Lee, 1994) and opposing input from (L+M) cones and project to the koniocellular layers of the LGN, which are situated between the parvocellular layers, in a distinct anatomical channel (K-pathway) (Dacey, 1999). Cone bipolar cells make connections with small bistratified ganglion cells only (Kouyama & Marshak, 1992) and they have large receptive fields (Dacey & Lee, 1994; Dacey et al., 1996). The inner dendrites of these ganglion cells connect with S-ON bipolars, and the outer dendrites connect with, L-M-OFF bipolars (Lee, 2004). According to Dacey (Dacey, 2000) the midget bipolar cells represent the S-OFF signals. Even though S-OFF signals have been recorded in LGN (Valberg et al., 1986), the S-OFF cells have not yet been identified morphologically. The previously identified bistratified structure is known to be a unique characteristic of S-ON cells, which are known to provide input to the koniocellular layers of LGN (Solomon & Lennie, 2007). Intracellular recordings have shown blue-ON/yellow-OFF opponent light responses as well (Dacey & Lee, 1994) and that bistratified ganglion cells receive direct ON input from S cones and OFF input from L and M cones (Dacey & Lee, 1994).

1.1.1.5 Amacrine Cells

Amacrine cells are also called ’laterally connecting interneurons’ and are located in the inner plexiform layer (**Figure 1.3**) (Dacey, 1999). Their exact role is uncertain, one possibility is that they provide a substrate for lateral inhibition (Wassle & Boycott, 1991) and they could also serve as a basis for cone opponent mechanisms (Dacey, 1999).

There are many different types of amacrine cell, two of them; A1 and A2 cells, have been extensively studied (Stafford & Dacey, 1997). A1 cells receive summed input from M and L cones and have a spiking ON-OFF response activity which probably contributes to the formation of the receptive field surrounds of the bipolar and ganglion cells (Dacey, 1999). A2 cells participate in the transmission of ON and OFF rod photoreceptor signals to the ganglion cells as well as signals from OFF-cone bipolars and OFF-midget bipolar cells (Dacey, 1999; Wassle & Boycott, 1991). None of these cell types receive significant input from S-cones (Dacey, 1999).

1.1.2 Lateral Geniculate Nucleus (LGN)

The LGN is located in the posterior part of the thalamus, receives most of its afferent inputs from the retina and functions partly as a relay station. The LGN contains six layers, each receiving a complete map of half a visual field of one eye (Derrington et al., 1984; Martin, 2004). Layers 1, 4, 6 receive information from the contralateral eye, layers 2, 3, 5 receive information from the ipsilateral eye. The layers are segregated and process different aspects of visual stimuli in anatomically and functionally distinct pathways (Derrington et al., 1984; Nassi & Callaway, 2009). The ventral layers (1 and 2) are known as the magnocellular layers and receive M retinal ganglion cell (parasol ganglion cells) inputs. The dorsal layers (3-6) are known as the parvocellular layers, and they receive input from P retinal ganglion cells (midget ganglion cells), which in turn receive input from midget bipolar cells (**Figure 1.5**) (Leventhal et al., 1981; Perry et al., 1984). The interlaminar (koniocellular) zones of the LGN are located between the M and P layers and receive input from K ganglion cells (small bistratified ganglion cells). Neurons in LGN have the same centre surround receptive field

organisation as the corresponding retinal ganglion cells and response properties of the afferent ganglion cells and the LGN cells are mostly the same (**Figure 1.5**) (Derrington et al., 1984; Desimone et al., 1984; Hubel & Wiesel, 1961; Kaplan et al., 1987). The cells in the parvocellular and koniocellular layers have strong chromatic opponent response properties (De Valois et al., 1966a; De Valois et al., 1958; Dreher et al., 1976; Wiesel & Hubel, 1966) and cells in the magnocellular layers give the strongest response to luminance modulations (**Figure 1.5**) (De Valois et al., 1966a; Livingstone & Hubel, 1988).

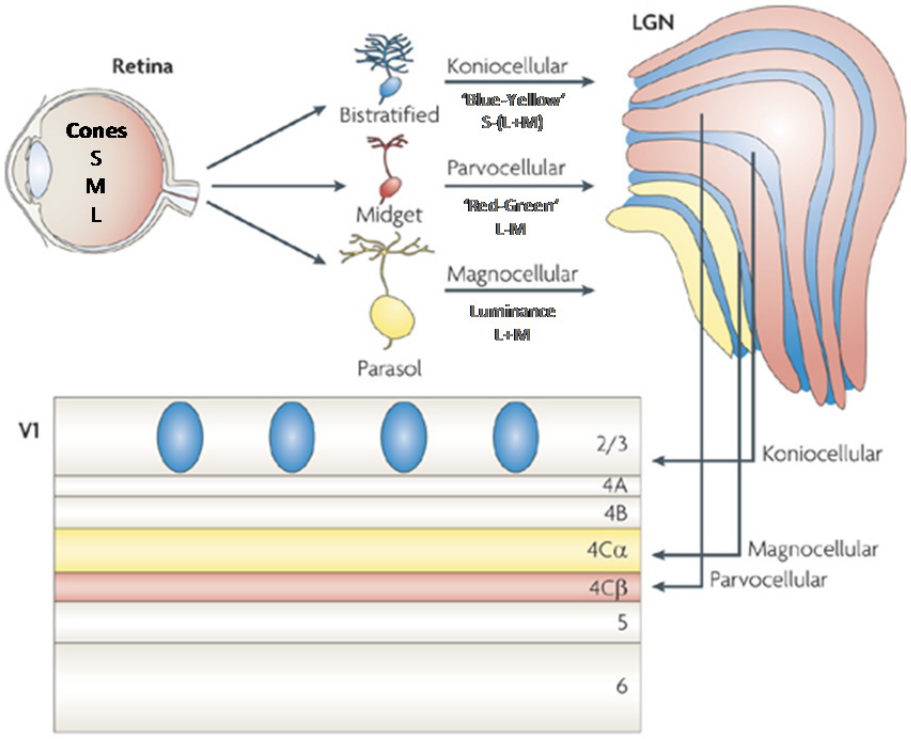


Figure 1.5 Parallel pathways in vision. The signals from the three cone opponent channels are transmitted through anatomically separate layers of the LGN to the Striate Cortex. From the LGN, midget ganglion cell signals are transmitted via the parvocellular layers to layer 4Cβ of V1. Parasol ganglion cells project to the magnocellular LGN layers and then to 4Cα of V1. Bistratified ganglion cell signals are carried to the cytochrome oxidase blobs in layer 2/3 in V1 via the koniocellular pathway (Source: (Nassi & Callaway, 2009)).

There are certain colour directions to which LGN neurons are tuned. Based on this, colour spaces were constructed where these directions are represented by the cardinal axes of colour space (**Figure 1.6**) (Derrington et al., 1984). The

cells that are devoted to the analysis of these cardinal colours are not only different in their chromatic properties but also anatomically separated into two distinct pathways. The parvocellular (P) pathway ('red -green'), carries opponent L and M cone inputs, whereas in the koniocellular (K) pathway ('blue-yellow') the summed input from L and M cones is compared with the S cone input (Casagrande, 1994). The magnocellular pathway represents the 3rd channel that processes luminance information (**Figures 1.5** and **1.6**).

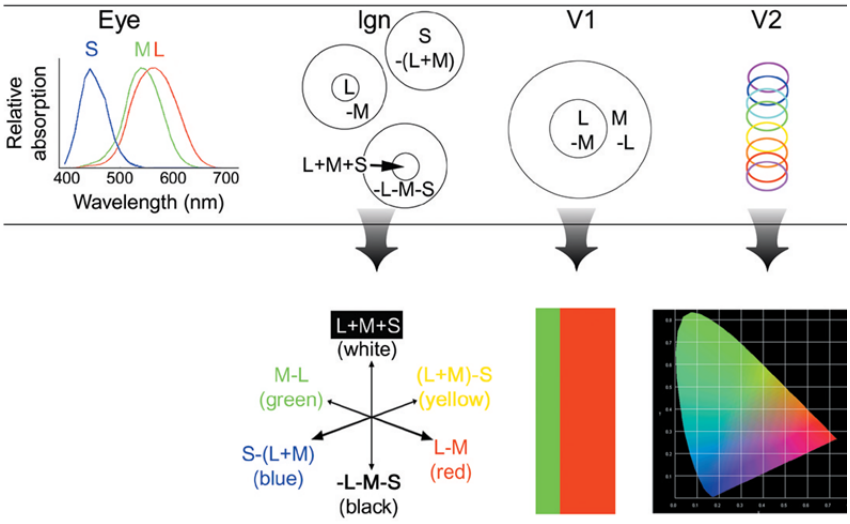


Figure 1.6 Schematic of colour processing in the visual system (Conway, 2003). The cones are activated by the incident light depending on their relative absorption. In the LGN, three cone opponent channels are formed via the comparison of cone signals; L-M ('red-green' cells), S-(L+M) ('blue-yellow' cells) and L+M (luminance). Double opponent cells are present in the visual cortex and contribute to chromatic contrast processing. In V2 perceptual hue categories are represented in localised bands along the thin stripes which might serve as a basis of hue perception (Source: (Conway, 2003)).

1.1.2.1 Magnocellular Layers

The magnocellular layers contain the largest cells in the LGN. These cells are located in the ventral layers (1, 2) and receive input from magnocellular (parasol) ganglion cells (**Figure 1.5**). They project to 4Cα and 4B layers of V1 (Hubel & Livingstone, 1990) and provide 10% of all cortical projections.

Magnocellular neurons mostly sum L and M cone signals (Derrington et al., 1984). M cells have reasonably large receptive fields, their receptive field centre

and surround receive input from the same mixture of cone types and they respond to a wide range of wavelengths. They have transient response characteristics, have high contrast sensitivity, show little sign of cone opponency and give a maximum response to low spatial and high temporal frequencies (De Valois et al., 2000a; Demonasterio & Gouras, 1975; Derrington & Lennie, 1984; Lee et al., 1989; Shapley et al., 1981; Wiesel & Hubel, 1966).

1.1.2.2 Parvocellular Layers

Parvocellular cells are located in the dorsal layers of the LGN and are connected with parvocellular (midget) ganglion cells providing 80% of the neurons in the LGN (Perry et al., 1984). They project to layers 4Cβ, 2 and 3 of V1 (**Figure 1.5**) (Hubel & Livingstone, 1990). P cells have small, spatially and colour (L/M) opponent centre surround receptive fields (Hendry & Reid, 2000; Reid & Shapley, 2002; Schiller & Malpeli, 1978; Wiesel & Hubel, 1966) and take part in the processing of both chromatic and achromatic information (De Valois & De Valois, 1993). They respond strongly to high contrast luminance and low contrast chromatic stimuli, meaning that they respond better to fine patterns and chromatic stimuli (Shapley et al., 1981).

Depending on their response properties there are three main types of cells that have been identified in the LGN so far (**Figure 1.7**) (Hubel & Wiesel, 1966). Type I cells have excitatory or inhibitory centres and antagonistic surround colour opponent receptive fields (Hubel & Wiesel, 1966). Their response properties are similar to the corresponding ganglion cell types. Type II cells do not have a centre surround receptive field structure but show colour opponent responses (‘colour opponent centre only’) (Hubel & Wiesel, 1966). Type III cells have ON and OFF centre receptive fields and both the centre and the surround

show the same spectral sensitivities ('broadband') (Creutzfeldt et al., 1979; Hubel & Wiesel, 1966; Hubel & Wiesel, 1968; Schiller & Malpeli, 1978).

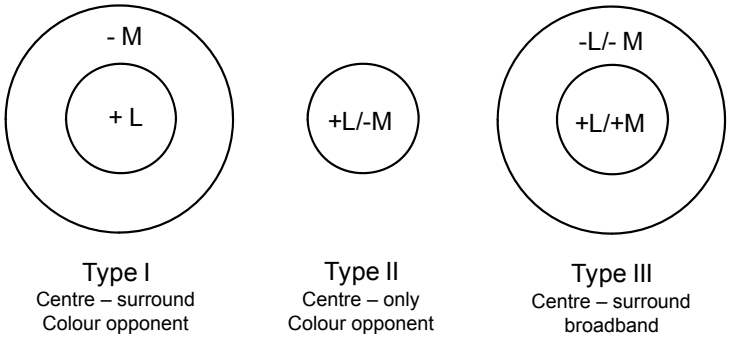


Figure 1.7 Illustration of the basic receptive field structure of neurons in the parvocellular layers of LGN. Type I cells receive excitatory input into their receptive field centre and inhibitory input into the receptive field surround, Type II cells receive opponent M and L cone signals into their receptive field centre. Type III cells receive mixed opponent input both to their centre and surround receptive fields.

1.1.2.3 Koniocellular Layers

The koniocellular layers are located in the interlaminar layers of the LGN and consist of very small cells (Hendry & Reid, 2000; Hendry & Yoshioka, 1994; Kaas et al., 1978) that project to the cytochrome oxidase (CO) rich blobs of the striate cortex (Hendry & Yoshioka, 1994; Hubel & Livingstone, 1990). In previous experiments the S-ON ganglion cells were found to have a bistratified structure (Chatterjee & Callaway, 2003; Hendry & Reid, 2000; Hubel & Wiesel, 1966; Kouyama & Marshak, 1992). S-ON cells receive excitatory S-cone signals and an opposing summed M and L cone input. The colour tuning of S-OFF cells is heterogenous, ranging on a scale between S-ON and red-green opponent neuron characteristics. The basis of these signals is still a matter of debate (Klug et al., 2003; Valberg et al., 1986).

1.1.3 Primary Visual Cortex (V1)

Most of the projections from LGN terminate in the primary visual cortex and only a minority of them connect directly with other cortical areas. There are many different types of cell in V1, organized to process orientation, movement, direction, colour, length, spatial frequency and contrast (Fries, 1981). V1 retinotopically represents the contralateral visual field with an extended representation of the fovea (Dow et al., 1981) and the topography of the visual field is preserved within these projections. The neurons are regularly arranged in laminae and columns with compartments that stain with cytochrome oxidase (CO) blobs. The cells are organized into six layers that are parallel to the cortical surface. Layer 1 mostly contains dendrites and axons, layers 2/3 contain excitatory neurons that connect with extrastriate areas (V2, V3, V4 and MT/V5). Layer 4 is subdivided into two main layers, 4B and 4C. 4Cα and 4Cβ receive the majority of LGN inputs. M cells project to 4B through 4Cα, and then to V2, and MT/V5 (**Figures 1.5** and **1.8**) (Blasdel et al., 1985; Callaway, 1998). These cells do not participate in colour processing (Kennedy & Bullier, 1985). Parvocellular layers from LGN project to 4Cβ and then to 4Cα, 4B and then to the CO rich blobs in layers 2/3 (Callaway & Wiser, 1996; Fitzpatrick et al., 1985; Yabuta & Callaway, 1998). K cells project to the CO rich blobs in layers 2/3, 4A and 4Cβ (Casagrande, 1994; Chatterjee & Callaway, 2003; Hendry & Yoshioka, 1994; Livingstone & Hubel, 1987).

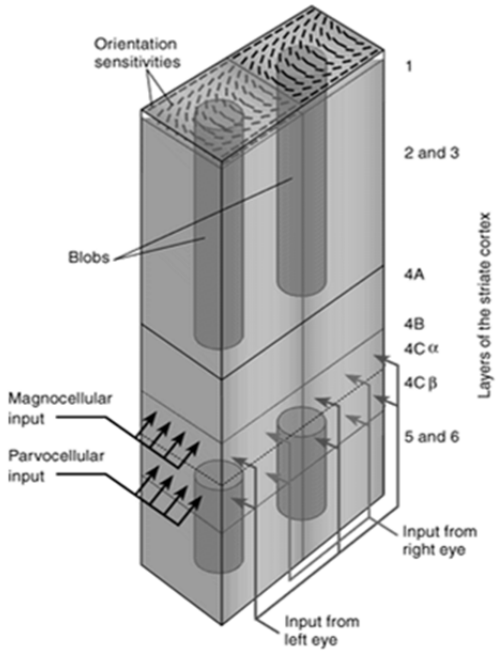


Figure 1.8 Schematic representation of the layers of V1. The cells in V1 are organised into layers that are parallel to the cortical surface and receive different inputs from LGN. The magnocellular and parvocellular layers from the LGN project to layers 4Cα and 4Cβ, respectively. The koniocellular layers of LGN provide input into the cytochrome oxidase blobs in layers 2/3. (Salinas, J. (n.d) [Online Image] Available at: <http://homepage.psy.utexas.edu/homepage/class/Psy308/Salinas/Vision/12.gif> [Accessed 23 Sept 2010]).

In V1 and V2 50% of the cells are colour selective (Gegenfurtner et al., 1996; Gouras, 1974; Kiper et al., 1997; Lennie et al., 1990; Yates, 1974), they process the sum of the inputs from the three different cones. Spatial and chromatic response properties of the opponent cells in V1 and V2 can be described based on the properties of LGN neurones (Derrington et al., 1984; Kiper et al., 1997; Lennie et al., 1990) (**Figure 1.6**). In V1 cells with double opponent receptive fields have been identified through electrophysiological studies (**Figure 1.9**). They receive two opponent cone signals to each of the centre and surround receptive fields (**Figure 1.9**) (Livingstone & Hubel, 1984; Shapley & Hawken, 2002), showing colour opponent responses when their receptive field centre or surround is solely stimulated. This double opponency is observed both in the blue-yellow and red-green pathway (Livingstone & Hubel, 1984).

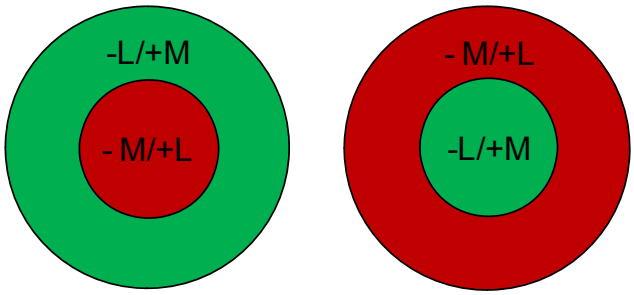


Figure 1.9 Illustration of L/M double opponent chromatic cells in V1. Both the centre and the surround of the receptive fields receive opponent cone signals. Note: colours are demonstrative and do not represent the actual wavelength of sensitivity for L/M opponent pathway.

Layer 4Cβ (lower part) contains colour opponent centre surround and broadband cells (Livingstone & Hubel, 1988). Cytochrome oxidase (CO) rich blobs in layers 2/3 contain centre only single opponent (Type II) and double opponent cells (Hubel & Livingstone, 1990; Livingstone & Hubel, 1984; Tootell et al., 1988). According to Chatterjee and Callaway (Chatterjee & Callaway, 2003), neurons that are tuned to 'blue-yellow' are located in layers 4A and 3B and CO blobs of V1, whereas 'red-green' neurons are located in layer 4C and project from LGN in a distinct channel. Layers 4Cα (upper part) and 4B are responsive to luminance modulations and do not respond to chromatic stimuli (Chatterjee & Callaway, 2003; Tootell et al., 1988). Conflicting with previous results, Leventhal et al. (Leventhal et al., 1995) did not find strict functional segregation for different stimulus attributes between the different layers.

The chromatic response properties of some V1 and V2 cells are not organized around the cardinal directions of colour space that represent subcortical colour processing (**Figure 1.10**) (Conway, 2003; De Valois et al., 2000a; Kiper et al., 1997; Lennie et al., 1990; Wachtler et al., 2003; Xiao et al., 2007; Yoshioka et al., 1996). Instead, these cells seem to be more tuned for colour categories that do not coincide with the cardinal axes specified by Krauskopf et al. (**Figure 1.10**) (Gegenfurtner & Kiper, 2003; Krauskopf et al., 1982). This implies that

there is a reorganization of colour processing away from cone opponent mechanisms at some stage between the LGN and cortical areas.

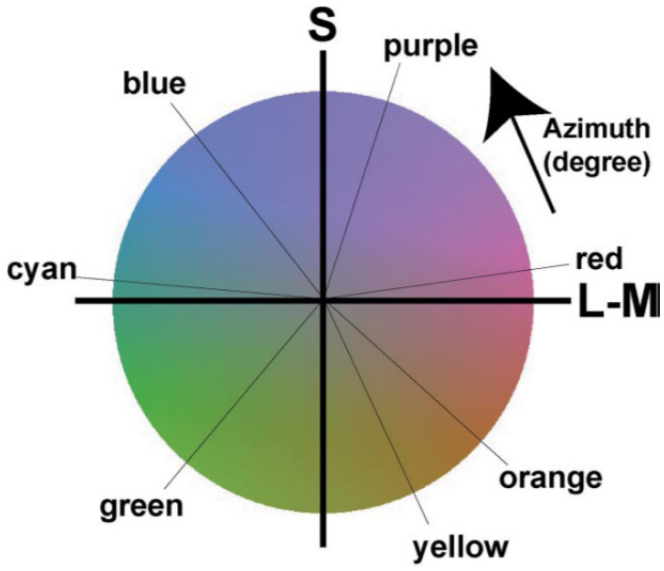


Figure 1.10 Isoluminant plane of the MBDKL (after MacLeod, Boynton, Derrington, Krauskopf and Lennie) colour space illustrating locations of the cardinal directions, perceptual colour categories and their relation to each other. The colours that are identified by the cone opponent colour processing do not coincide with the perceptual colour categories. Some cells in the Visual Cortex are tuned to perceptual colour categories as opposed to the cone opponent processing (Derrington et al., 1984; Gegenfurtner & Kiper, 2003; Krauskopf et al., 1982; Lennie et al., 1990; MacLeod & Boynton, 1979) (Source: (Gegenfurtner & Kiper, 2003)).

According to Conway (Conway, 2003), perceptual processing on the basis of colour categories starts at the level of V2 in the cytochrome oxidase (CO) stripes. However, the recent results of Xiao et al. (Xiao et al., 2007) suggest that there are neurons, not only in V2, but also in V1, that are tuned to different hues (**Figures 1.6 and 1.10**). They presented spatially uniform stimuli to macaques and recorded the intrinsic optical signals in the striate cortex using an optical imaging technique. Each of the presented stimuli resulted in the activation of neurons in a well circumscribed area in V1. The locations of the peak neural activations corresponded with the different hues that were presented. These clustered cells, which were tuned to different colours, formed maps in V1 (**Figure 1.11**).

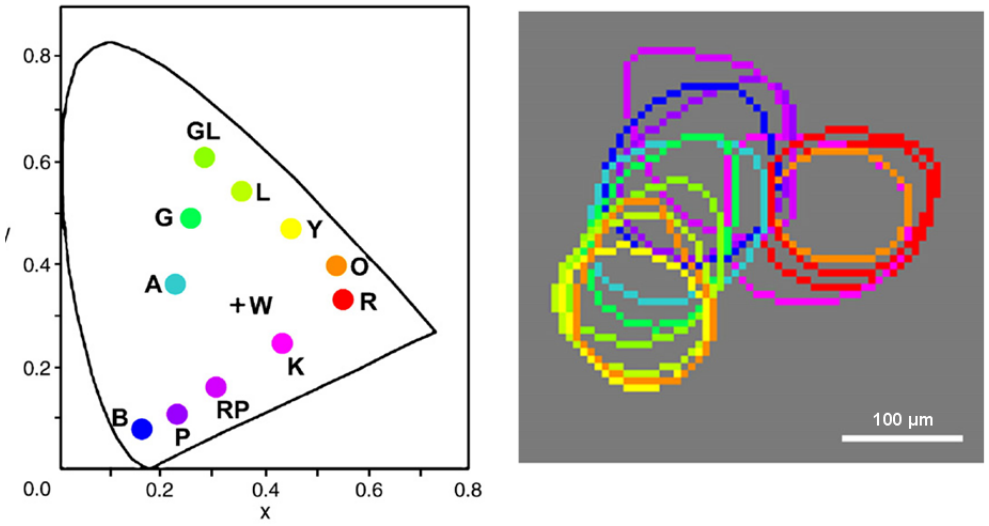


Figure 1.11 Spatially organised hue maps in the striate cortex, recorded with an optical imaging technique. The figure illustrates the CIE 1931 xy coordinates of the presented stimuli and the outlines of the response regions that showed activation in response to the stimulus colours (Source: (Xiao et al., 2007)).

1.1.3.1 Visual Area 2 (V2)

Colour information is next processed in area V2. As well as other areas of the brain, V2 is connected with V1, LGN and the pulvinar (**Figure 1.12**) (Bullier & Kennedy, 1983; Curcio & Harting, 1978). Recent studies have shown that the different layers are segregated to a different extent (Shipp & Zeki, 2002), contradicting earlier results that found little segregation in V2 (Johnson et al., 2001; Leventhal et al., 1995). Shipp and Zeki state that there is a higher degree of differentiation in the middle layers, which receive input from V1, and lesser differentiation in the outer layers, which have connections with other cortical areas (Shipp & Zeki, 2002). V2 consists of 26-34 parallel, pale, dark thick and dark thin stripes perpendicular to V1. The signals from V1 to the thin and thick stripes are independent of each other and different anatomical channels convey distinct perceptual information (Sincich & Horton, 2005). CO blobs in layers 2 and 3 of V1 provide input into dark thin stripes, the interblob regions of V1 project to the pale interstripe regions and layer 4B provides input into CO rich

dark thick stripes of V2 (Livingstone & Hubel, 1988; Livingstone & Hubel, 1983, 1987). Thick stripes in turn project to MT and V3 (DeYoe & VanEssen, 1985; Shipp & Zeki, 1985) and thin and interstripe layers project to V4 (DeYoe & VanEssen, 1985; Shipp & Zeki, 1985). Most of the neurons in the thin stripes are selective for chromatic stimuli, double opponent and have connections with V4 (**Figure 1.12**) (Gegenfurtner, 2003; Gegenfurtner et al., 1997; Roe & Tso, 1995; Shipp & Zeki, 1985; Tootell et al., 2004), whereas thick and pale stripes are tuned for direction (thick), orientation discrimination (thick, pale stripes), stereoscopic depth (thick stripes) and project to MT (Sincich & Horton, 2005; Vanduffel et al., 2002). According to recent findings in the macaque using optical imaging techniques, colour selective neurons are organized into modules in the thin cytochrome oxidase stripes of V2. They respond selectively to different colours and the colour of a stimulus is located by peak responses of the neurons to a certain colour. These peak responses result in a spatially organized colour map in V2 (Conway et al., 2007; Xiao et al., 2003).

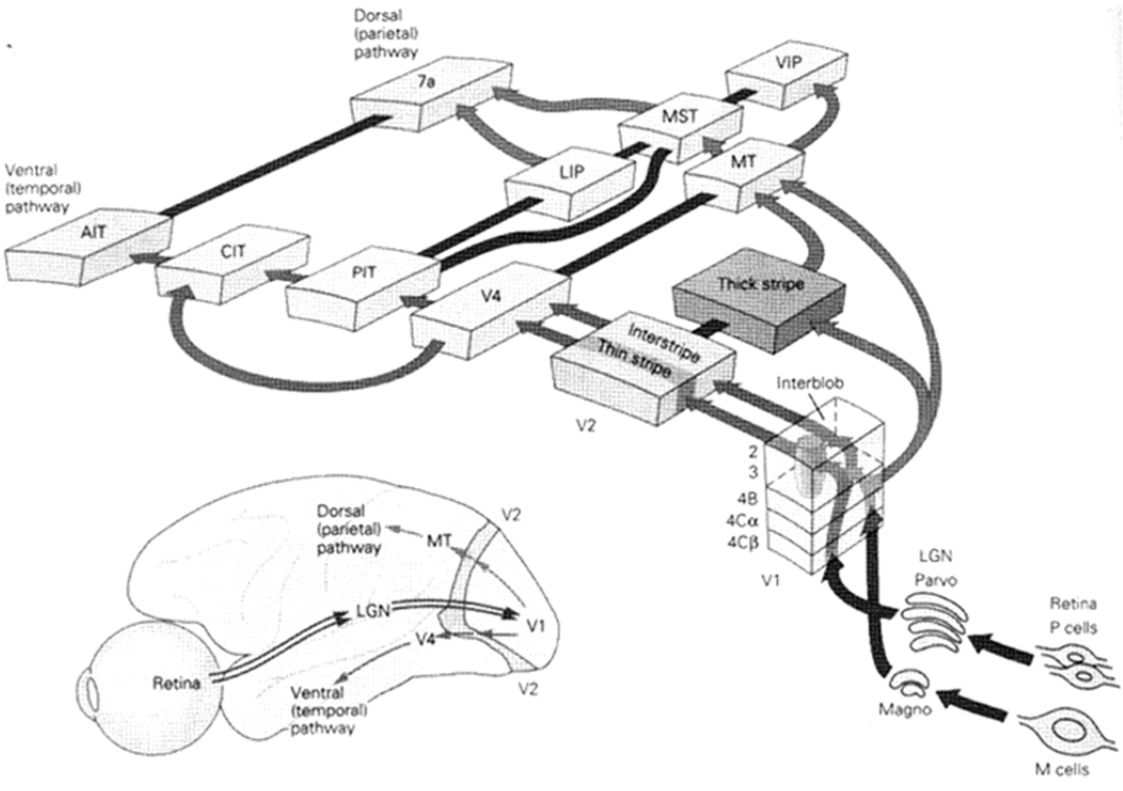


Figure 1.12 Schematic of the visual pathways in the brain. The magnocellular and parvocellular pathways project separately from the retina through the LGN to the Visual Cortex. There are also separate pathways from V1 to the parietal and temporal lobes forming the dorsal and ventral pathways, respectively. Abbreviations: CIT = Central Inferior Temporal Area, LIP = Lateral Intraparietal Area, MST = Medial Superior Temporal area, MT = Middle Temporal area, PIT = Posterior Inferior Temporal area, VIP = Ventral Intraparietal area
(Sereno M. (n.d.) [Online Image]
Available at: <http://kamares.ucsd.edu/~ffilimon/107B/107b.html> [Accessed 23 August 2010]).

1.1.3.2 Visual Area 3 (V3)

V3 consists of two divisions, ventral (V3v) and dorsal (V3d) in rhesus monkeys (Zeki, 1978), but it is still a matter of debate whether they are anatomically and functionally distinct (Wandell et al., 2005; Wandell et al., 2007; Zeki, 2003). Neurons project to V3 from 4B layer of V1 via the thick stripes of V2, which suggests a role in magnocellular information processing (Felleman et al., 1997a; Girard et al., 1991). However, V3 also receives inputs from V1 that are related to parvocellular processing (Gegenfurtner et al., 1997).

Neurons in V3 are organized into functional preference columns in rhesus monkeys (Zeki, 1974). V3 cells are mostly motion, colour (Dubner & Zeki, 1971;

Felleman & VanEssen, 1987; Gegenfurtner et al., 1997) and direction selective (Dubner & Zeki, 1971). They respond maximally to low spatial and high temporal frequencies when compared to V2 cells (Gegenfurtner et al., 1997). V3v also takes part in the processing of the direction of gaze and object motion (Galletti et al., 1990; Tootell et al., 1997). There are as many colour selective cells in V3 as in V2 (about 50%), and there is a considerable overlap between the cells that process chromatic information and the cells that process motion (Gegenfurtner et al., 1997). Moreover, some of these cells are involved in the processing of motion which is defined by colour (Essen & Zeki, 1978; Gegenfurtner et al., 1997). However, according to recent research, V3 has only limited function in colour vision (Conway & Tsao, 2006).

According to Gegenfurtner et al. (Gegenfurtner et al., 1997) this area has extensive connections with MT and V4, therefore it might represent a stage where different dimensions of visual processing are integrated and coordinated. It also has afferent connections with the posterior intraparietal area (PIP) and medial superior temporal area (MSTd) (Felleman et al., 1997a).

1.1.3.3 Visual Area 4 (V4)

Macaque V4 was first identified by Zeki using single unit recordings. It is believed to show similarities to human V4 in terms of containing a considerable amount of colour selective cells (Zeki, 1973). According to macaque lesion studies, V4 receives the majority of inputs from V1, V2 (thin and interstripe regions) and V3 and mainly projects to the temporal occipital area (TEO) in the inferotemporal cortex (**Figure 1.12**) (Distler et al., 1993; Felleman et al., 1997b; Tanaka et al., 1990). V4, in the macaque, is divided into two subregions; the posterior part receives inputs from the thin and pale stripes of V2, and the

anterior division receives its inputs mainly from the posterior part (DeYoe & VanEssen, 1985; Shipp & Zeki, 1985; Zeki, 1990). According to electrophysiological studies on macaques, V4 neurons are not only selective for colour but also for other aspects of spatial vision such as orientation, length and width of bars (Desimone & Schein, 1987; Zeki, 1977). Cells that are selective for orientation receive inputs from the interstripe areas of V2 and are also selective for colours to a certain extent (Desimone & Schein, 1987; Zeki, 1973, 1977). Colour selective cells in turn receive inputs from the thin stripes of V2 (Zeki & Shipp, 1989). This leads to the conclusion that, as in V1 and V2, colour and form are processed together in V4 (Cheng et al., 1994; Desimone & Schein, 1987; Ferrera et al., 1994). V4 is also capable of processing complex features (Gallant et al., 1996; Hanazawa & Komatsu, 2001; Kobatake & Tanaka, 1994; Pasupathy & Connor, 1999).

Based on human brain imaging and clinical lesion studies, human V4 was located in the lingual and fusiform gyri (Lueck et al., 1989; McKeefry & Zeki, 1997b). For many years it was regarded as the colour centre of the human brain (Zeki, 1990). Results from human brain imaging studies also suggest that it is a brain area that is responsible for colour constancy, a phenomenon that allows colour perception to be the same under different light conditions (McKeefry & Zeki, 1997b; Zeki et al., 1999; Zeki & Bartels, 1999).

1.1.3.4 Inferotemporal Cortex (IT)

V4 has many afferent projections into different parts of the brain, such as areas in the Posterior Inferotemporal Cortex (PITd, PITv) (Felleman et al., 1997b). This region of the brain is mostly involved in the processing of more complex stimulus patterns (Kobatake & Tanaka, 1994), such as shape (Felleman et al.,

1997a), faces (Desimone et al., 1984) and familiar objects (Sakai & Miyashita, 1994) and a high proportion of the cells is colour selective (Conway, 2009; Desimone et al., 1984; Komatsu et al., 1992). Lesion studies also support the role of this region in colour vision as its lesion results in cerebral achromatopsia among the loss of other higher order visual functions (Gegenfurtner, 2003).

According to Conway and Tsao (Conway & Tsao, 2006), the dorsal part of the Posterior Inferotemporal cortex (PITd) of macaques is highly colour selective and could be responsible for the integration of colour signals. Lesion studies also supported this fact; large lesions that affect the PITd, impair colour vision (Conway & Tsao, 2006).

The Posterior Inferotemporal Ventral area (PITv) also has a variety of feedback and feed-forward connections with V4 (**Figure 1.12**) (Felleman et al., 1997b). There are many cells with complex receptive field properties (they respond to combinations of shape and colour), and others have simple receptive field properties. There are clusters of cells in PITv that are selective for either colour or orientation (Kobatake & Tanaka, 1994).

1.2 Spatial Vision

1.2.1 Introduction

Spatial vision refers to the ability of the visual system to discriminate features of the environment based on the distribution of the light intensity reflected into the eye. Spatial vision ultimately leads to object recognition and scene interpretation and is a fundamental feature of visual processing. The two main measures of spatial vision are visual acuity and contrast sensitivity. Visual

acuity describes the ability to resolve the smallest details of high contrast stimuli, whereas contrast sensitivity defines the lowest contrast needed between two stimuli in order for the visual system to be able to perceive them as different.

Spatial vision has traditionally been examined using sine-wave luminance grating stimuli (**Figure 1.13**). These stimuli have certain key parameters which define them. Spatial frequency is defined by the number of dark/light cycles in a luminance pattern, per 1° of visual angle (c/deg). Contrast is the amplitude of the wave relative to its mean that is expressed by the Michelson contrast:

$$C = \frac{L_{max} - L_{min}}{L_{max} + L_{min}} \tag{1.1}$$

Where, L_{max} and L_{min} represent the luminance values of the peak and the trough of the waveform, respectively.

The luminance of a one dimensional sine-wave grating at any point(x) can be expressed by:

$$L(x) = L_m\left[1 + c\sin(2\pi fx + \phi)\right] \tag{1.2}$$

Where, L_m is the mean luminance, c is the contrast, f is the spatial frequency, and ϕ is the spatial phase.

Two luminance sine-wave gratings can be different in terms of spatial frequency, amplitude, contrast, phase, orientation and colour (**Figure 1.13**). According to Fourier (Fourier, 1823), with a procedure called Fourier Analysis, any two-dimensional signal can be broken down into a linear set of harmonic sinusoidal gratings, which are described by specific spatial frequency, amplitude, phase and orientation.

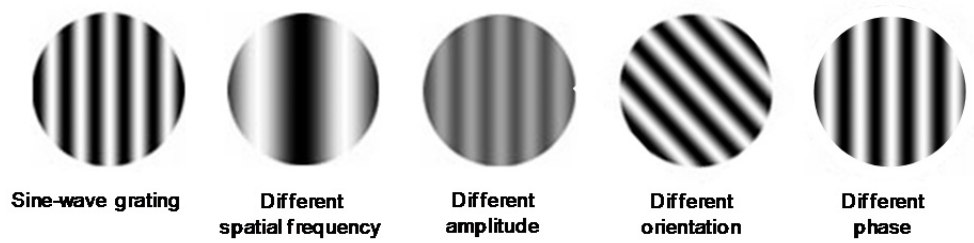


Figure 1.13 Illustration of sine-wave gratings of lower spatial frequency, different amplitude, orientation and phase (Source: (De Valois & De Valois, 1988)).

1.2.2 Contrast Sensitivity Function

The ability of the visual system to perceive detail depends on the contrast and size of the stimulus (Campbell & Robson, 1968). Contrast detection thresholds are measured in order to define the relationship that is required by the visual system, between the size and the contrast, in order to be able to perceive a visual stimulus. Contrast sensitivity equals to the reciprocal of the contrast detection threshold, and contrast sensitivity function (CSF) is the variation of contrast sensitivity of the observer to luminance sinusoidal gratings along a given variety of spatial frequencies. The maximum of the function occurs between 2-6 c/deg and the sensitivity decreases both towards higher and lower spatial frequencies (**Figures 1.14 and 1.15**). In the case, when there are less than 4 cycles of the grating are visible, the contrast detection thresholds rise significantly. On the other hand, high spatial frequencies (above 10 c/cm) result in a significant reduction of the contrast as a result of the limitations of the display equipment (**Figure 1.14**).

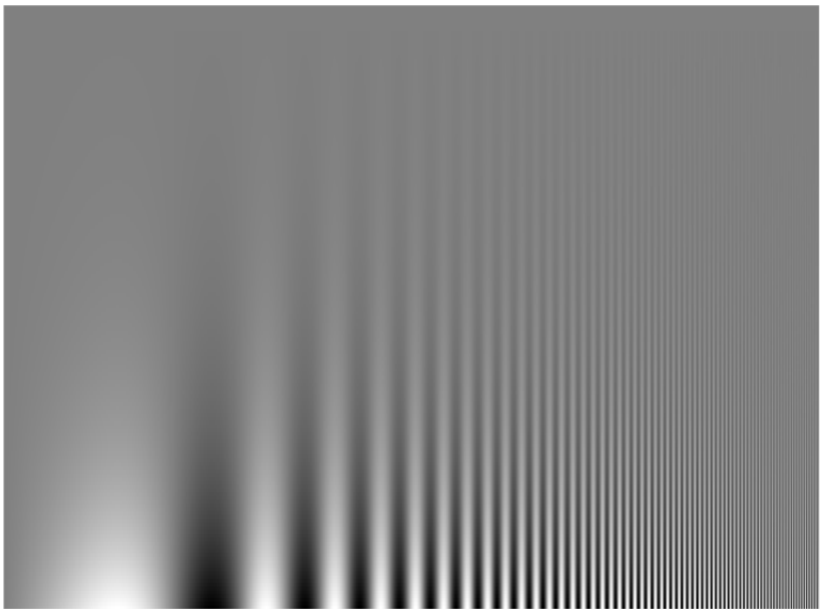


Figure 1.14 Illustration of how contrast sensitivity function (CSF) changes as a function of the size and contrast of the stimulus in humans. This typical inverted U shape of the CSF illustrates the perceptual capabilities of the visual system. Even though the contrast is the same at any point, sampled along any horizontal line, the bars in the middle are perceived to be taller than the ones on either side, which implies that less contrast is needed at medium, as compared to high spatial frequencies to detect a sinusoidal grating (Campbell & Robson, 1968).

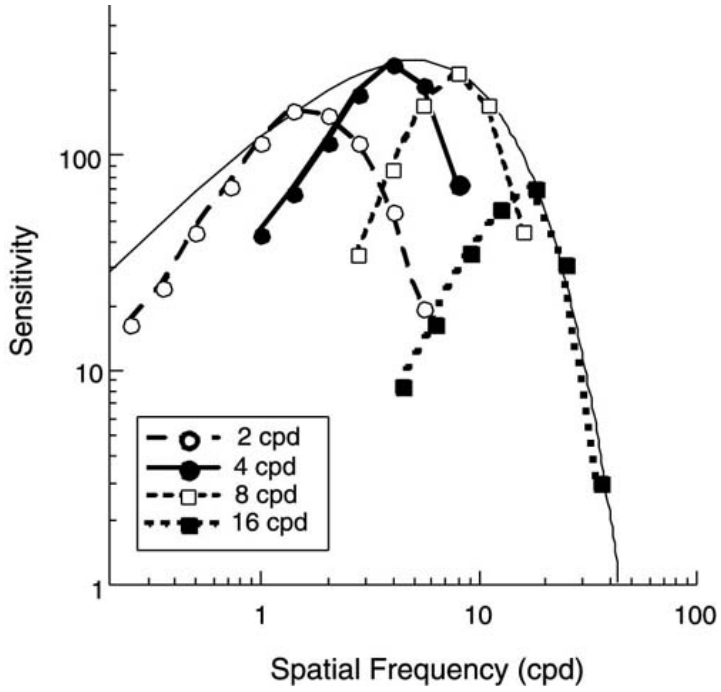


Figure 1.15 The sum of several narrowly tuned spatial frequency channels make up the spatial contrast sensitivity function (CSF). CSF is determined by the individual sensitivities of neurons responsive to limited ranges of spatial frequency in V1. The maximum of the function falls between 2-6 c/deg and the sensitivity gradually decreases towards lower and steeply decreases at higher spatial frequencies (Source: (De Valois & De Valois, 1988)).

There is also a substantial amount of variation in the contrast sensitivity function with changing luminance levels and increasing retinal eccentricities. As luminance increases, the peak of the CSF is shifted towards higher spatial frequencies. Similarly, there is a shift of the peak of the function from 6 c/deg to 2 c/deg when light conditions change from photopic to mesopic, which results in the loss of contrast sensitivity at high spatial frequencies. Increasing retinal eccentricity results in similar changes as reduced luminance levels.

1.2.3 The Eye as an Optical System

The optics of the eye is able to convey a maximum of 60 c/deg spatial frequency, which is called the optical limit of resolution. The density of cones is greatest in the central retina, whereas rods are absent in the fovea and most dense in the periphery at approximately 20°. Each photoreceptor samples a discrete part of the retinal image and in the central retina, the presence of approximately 120 receptors per degree of visual angle (300 μm) is sufficient for optimal spatial resolution, to represent a wide range of spatial frequencies. This spacing equals to 2.5 μm distances between the centres of the photoreceptors (Polyak, 1957). Cone density rapidly decreases towards the periphery, to around 20 cones/deg at approximately 10° away from the fovea. This results in a decreased ability to perceive high spatial frequencies in peripheral vision.

The combined activation of the three cones results in the colour signals. If we consider the red-green pathway (L-M), the inter-receptor distance increases twofold as compared to luminance vision, simply because of the constraints of the receptor spacing. In case of blue-yellow (S-(L+M)), the situation is less optimal, both because of optical factors and receptor spacing. For these

reasons the colour CSF has a lower resolution limit compared to the luminance CSF.

The cone signals are transmitted to the bipolar cells, via a 1-1 cone specific connection in the central retina, which remains unaltered in the periphery. At the level of the ganglion cells, the size of the receptive field centres increase with increasing eccentricity.

1.2.4 Spatial Vision in the LGN

Cells in the P and M pathways process spatial position and spatial frequency, and it is always the size of the smallest receptive field centre that establishes the highest spatial frequency that the visual system can resolve (Shapley & Lennie, 1985). The receptive field sizes of M and P cells increase with eccentricity, therefore spatial frequency tuning curves shift to lower spatial frequencies in the periphery.

A typical LGN cell would give maximal response for a grating where the half cycle (width of the light bar) corresponds with the receptive field centre. In case of a uniform field of the equivalent mean luminance, the same cell would respond with central depolarization, and a decrease in hyperpolarization, which would overall result in a much larger depolarization. In case of a lower spatial frequency grating, part of the light bar will fall on the surround, increasing hyperpolarization, which would in turn cancel some of the depolarization of the centre of the receptive fields, resulting in an overall smaller depolarization of the cell. A higher spatial frequency grating, or a grating of different phase would also result in an attenuated response.

1.2.5 Spatial Vision in the Cortex

Cells in the visual cortex (simple and complex cells) are responsive to specific geometric features that fall within their receptive fields, but the firing rate varies depending on spatiotemporal factors, such as contrast, spatial position, temporal frequency, colour, orientation, wavelength and motion. These cells can be imagined as multidimensional filters, which select certain dimensions of an image, such as spatial frequency (Van Essen et al., 1992). The range of spatial frequencies a cell is responsive to is expressed as the bandwidth, and is measured in octaves. It is well known that retinal ganglion cells respond to a reasonably wide range of spatial frequencies, therefore they are regarded as having broad bandwidths. According to measurements, the bandwidth of ganglion and LGN cells is around 5 octaves (De Valois & De Valois, 1988). Electrophysiological studies found that V1 neurons respond selectively to a narrower range of spatial frequencies (Blakemore & Campbell, 1969a; De Valois et al., 1982a; Hubel & Wiesel, 1962). The fact that the relatively broad bandwidth of the LGN cells narrows down to 1.4 octaves at the level of striate cortex (the range is 0.7-3, with a population mean of 1.4, which equals to the pooled discrimination ability of the neurons), implies that cells here are tuned to a more limited range of spatial frequencies and the optimal spatial frequency falls between 2-8 c/deg (De Valois et al., 1982a; Shapley & Lennie, 1985).

Some information is lost at the level of the cortex due to nonlinear mechanisms, such as contrast gain control and response expansion. However, these mechanisms improve stimulus selectivity of the cortical neurons. Neurons here respond to narrower wavelength ranges, and usually are selective to a number

of dimensions (spatial position, orientation, spatial frequency, contrast, temporal frequency, direction of motion and colour).

Neurons in striate cortex can also be subdivided into three categories; simple, complex and hypercomplex cells, according to their receptive field properties, as found in studies on monkeys (Hubel & Wiesel, 1959, 1962; Hubel & Wiesel, 1968).

1.2.5.1 Simple Cells

Simple cells have distinct excitatory and inhibitory receptive fields. They linearly process antagonistic signals, which arise from their receptive fields. A stimulus that excites the whole receptive field results in a larger response than a smaller one. Simple cells respond to oriented bars, luminance edges, and their maximum response arises when the bars are parallel to the boundary of the cell (Skottun et al., 1991).

1.2.5.2 Complex Cells

Complex cells, like simple cells have elongated receptive fields. Their response properties are the same for increments and for decrements of light. They show selective activation to direction and orientation. They do not have different excitatory and inhibitory areas, and respond equally well to a suitably oriented stimulus (moving lines, edges), regardless of its location in the receptive field (Hubel & Wiesel, 1959). Response characteristics of complex cells cannot be explained by simple addition or extraction of light (Skottun et al., 1991).

1.2.5.3 Hypercomplex Cells

The receptive fields of hypercomplex cells are more selective. They have inhibitory and excitatory areas but there is an additional inhibitory zone at each

end of the excitatory zones. They respond to bars, the length of which determines the strength of their activation (Hubel & Wiesel, 1968; Hubel & Wiesel, 1977). They are the most suitable for the detection of the spatial frequency of objects (Skottun et al., 1991).

1.2.6 Multiple Processing Channels

There is ample evidence that there are multiple mechanisms in human spatial vision, each devoted to the processing of a narrow range of spatial frequencies (**Figures 1.15** and **1.16**) (Blakemore & Campbell, 1969b; Campbell et al., 1978; Campbell & Robson, 1968; Pantle & Sekuler, 1968) and these multiple mechanisms together make up the contrast sensitivity envelope. These channels are in fact groups of cells that can be imagined as filters that select information and only pass those, which coincide with the selective spatial frequency sensitivity range of that specific channel (Hubel & Wiesel, 1962). The selectivity can be quantified by a specified bandwidth-range of spatial frequencies the cell is responsive to. The term ‘band-pass’ is used to describe these channels and refers to the fact that it selects a specific frequency range and refuses others. ‘High-pass’ filters are selective for high spatial frequencies, whereas ‘low-pass’ ones let through low spatial frequency information. The median spatial frequency bandwidth of the cortical neuron population is 1.4 octaves. The human visual system is most sensitive at 2-8 c/deg and the sensitivity decreases at higher or lower spatial frequencies, resulting in the ‘band-pass’ shape of the CSF, as described before (**Figure 1.16**) (Campbell & Robson, 1968; De Valois et al., 1974; Goris et al., 2009). In case of low spatial frequencies, the reduction of the CSF is most likely a result of lateral inhibition (Donner & Hemila, 1996; Enroth-Cugell & Robson, 1966), whereas at high

spatial frequencies the sensitivity is limited by the ocular optics, as well as the poor signal to noise ratio in these channels and the limitations of spatial resolution inherent in the size and spacing of the retinal receptors (Banks et al., 1987; Campbell & Gubisch, 1966; Curcio et al., 1987; Packer & Dacey, 2000; Rovamo et al., 1994; Rovamo et al., 1978).

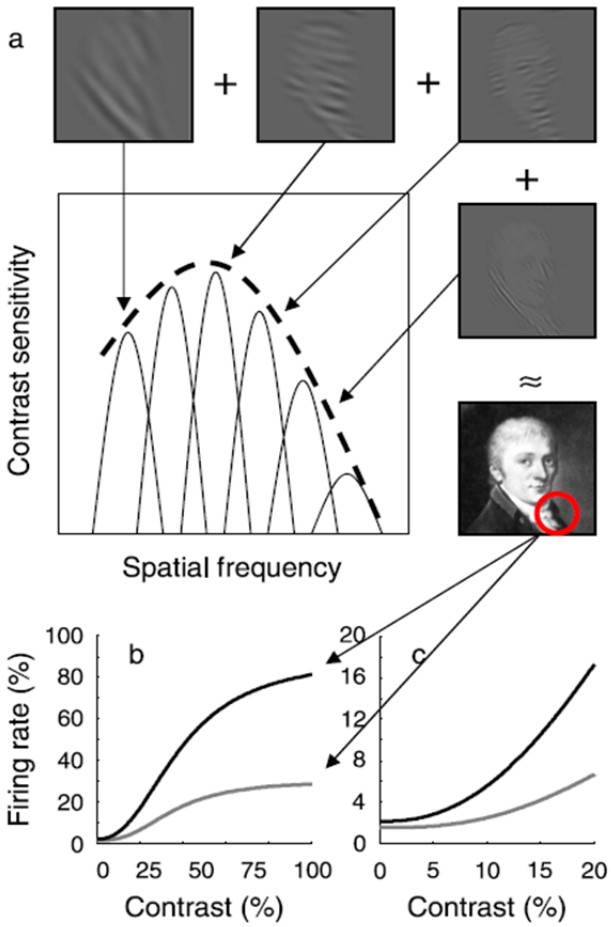


Figure 1.16 The multi-channel model of spatial vision. Figure a) illustrates narrow-band responses of channels to the spatial frequency content of example images. The dashed line represents the summed contrast sensitivity function. On figure b) the simulated contrast response functions of two exemplar cortical cells are shown as indicated by cell firing rate changes as a function of contrast. These cells show spatial-frequency and orientation selective filter characteristics. The figure illustrates that the two filters/cells show different sensitivity to narrow-band stimuli. The cell that is tuned to the presented orientation and spatial frequency shows the highest response activity at all contrast levels. Figure c) shows the response characteristics of these cells at low contrast levels (Source: (Goris et al., 2009)).

Neurophysiological (De Valois et al., 1982a) and psychophysical (De Valois & Switkes, 1983; Graham & Nachmias, 1971; Graham et al., 1978; Magnussen & Greenlee, 1985; Stromeyer & Julesz, 1972) experiments that employed pattern specific adaptation (Blakemore & Campbell, 1969a; Pantle & Sekuler, 1968) and masking techniques have provided evidence for the existence of these multiple channels. Masking and adaptation effects are probably based on the same neural processes, the only difference being is that the masking has a

shorter timescale but the initial effects are of the same amplitude (Georgeson & Georgeson, 1987).

1.2.6.1 Adaptation Experiments

In essence, during adaptation, a neuron is activated by its preferred stimulus for a prolonged time, which results in transmitter depletion, and the response of the neuron will transiently be attenuated to subsequent stimulation (Albrecht et al., 1984). This will result in an overall reduction of sensitivity towards the adapted stimulus (**Figure 1.17**). Another possible mechanism behind adaptation is contrast gain control in the striate cortex (Geisler & Albrecht, 1992), denoting that the cells amend their sensitivity to the level of the average contrast of the stimulus which is being processed within their RF, resulting in the enhancement of the sensitivity in case of low contrast stimuli, and lessening of sensitivity when they encounter high contrast ones.

Blakemore and Campbell (Blakemore & Campbell, 1969a) were the first to attempt to quantify the bandwidths of the channels by employing a psychophysical method called spatial frequency adaptation. During these experiments the observer is presented with a high contrast sine wave grating of a given spatial frequency and orientation. After adaptation takes place, contrast detection threshold for gratings that have the same orientation, spatial frequency but lower contrast will be elevated. The magnitude of the elevation of the detection threshold depends on the contrast of the grating the observer is adapted to. However, the characteristic shape of the adaptation effect is always the same, independent of the contrast (**Figure 1.17**) and threshold elevation does not take place if the adaptor grating has different orientation or its spatial frequency differs by an octave (Blakemore & Campbell, 1969a; Pantle &

Sekuler, 1968; Switkes et al., 1988), which confirms the idea of the multiple narrowly tuned channels for spatial frequency (Campbell & Robson, 1968). The bandwidth of the effect is approximately 1 octave (at half amplitude) and the amplitude is similar for every channel. The bandwidth is the same within the spatial frequency range of 3-14 c/deg. Higher frequencies result in a narrower range and lower frequencies all have their peak effect at 3 c/deg.

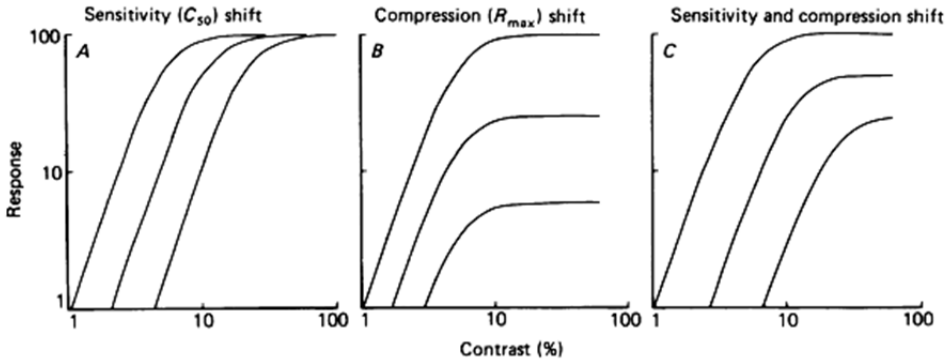


Figure 1.17 Illustration of how contrast adaptation could potentially affect the contrast response function of striate neurones. Figure A) shows sensitivity shift, namely, the contrast adaptation shifts the response range horizontally to the right, meaning that higher contrast levels are required in order to elicit the same neural response. Section B) shows compression shift, according to this, adaptation to contrast results in a shift of the curves vertically and downward; implying that the maximum rate of response decreases. Section C) shows the additive effect of sensitivity and compression shift (Source: (Albrecht et al., 1984)).

Shifts in the matched (perceived) spatial frequency were also found after exposure to an adaptor of a given spatial frequency (Blakemore et al., 1970). Gratings that have higher spatial frequencies than the adaptor appear to have even higher spatial frequencies, and gratings of lower spatial frequencies than the adaptor are perceived as having even lower spatial frequencies (Blakemore et al., 1970). The amplitude of this effect elevates as the contrast or the presentation time of the adaptor is increased (Greenlee et al., 1990). It has also been found that only gratings of the same orientation are capable of evoking this effect. This adaptation is tuned to a certain spatial frequency, the bandwidth of which is around 1.4 octaves, which is in agreement with other spatial

frequency contrast adaptation experiments (Georgeson & Harris, 1984), and coincides with the median bandwidth of the cells in the striate cortex. No shifts were found in cases when the adaptor and the examined grating had the same spatial frequency or when they differed by more than 2 octaves (Blakemore et al., 1970).

1.2.6.2 Masking Experiments

Masking experiments provided further psychophysical evidence in favour of the existence of multiple spatial frequency selective channels. The basic assumption behind these results is that a lack of effect of the mask on the detectability of the test confirms that the examined information (stimulus attributes) is processed via separate channels. During these studies, detectability of a stimulus is measured with and without the presence of a mask stimulus. The examined stimulus dimensions of the masks can be varied in order to examine the extent to which interactions are involved. These studies found spatial frequency selective masking, namely, the mask was only 'effective' within a range of $\pm$ 1.5 octaves around the examined stimulus spatial frequency (De Valois & Switkes, 1983; Henning et al., 1981; Stromeyer & Julesz, 1972), a result which further confirms the existence of multiple, independent processing channels.

Klein et al. (Klein et al., 1974) presented two gratings concurrently, a central circular one, and a non-overlapping annulus surrounding it, and found that the perceived spatial frequency of a grating was altered by the spatial frequency of the surrounding annulus. In the case when the inner spatial frequency was higher, it was perceived as even higher, and in case when the inner grating had lower spatial frequency than the surround, it appeared to have an even lower

spatial frequency. The direction of these shifts is in agreement with previous results (Blakemore et al., 1970; Blakemore & Sutton, 1969).

1.2.6.3 Orientation Selectivity

Masking experiments (Campbell & Kulikowski, 1966; Campbell et al., 1966) have shown that, as opposed to gratings of similar orientations, in cases when mask orientation is different from the test, contrast detection thresholds for a grating of similar spatial frequency are not elevated. However, similar orientations (within a given range) do have an effect. Spatial frequency shifts and contrast sensitivity loss arise as a result of adaptation only in similar orientations to the adapted spatial frequency (Blakemore & Campbell, 1969a, 1969b; Blakemore & Nachmias, 1971; Sekuler et al., 1968). In other words, if the visual system is adapted to a high contrast spatial frequency of a given orientation, the contrast sensitivity will temporarily decrease for gratings of the same spatial frequency and orientation, but not in cases where the orientation of the grating is different (Blakemore & Nachmias, 1971; Gilinsky, 1968; Sekuler et al., 1968). This orientation bandwidth was found to be 24°-30°. However, Blakemore and Nachmias (Blakemore & Nachmias, 1971) and Movshon et al. (Movshon et al., 1978) found a bandwidth of 15° independent of spatial frequency, which is quite narrow compared to the results of the masking experiments suggesting an inherent factor in the measurement method. Suprathreshold summation experiments found an even narrower bandwidth of 6° (Kulikowski et al., 1973). However, results indicating the very narrow tuning are not in agreement with the tuning characteristics of the cells in the striate cortex.

Orientation selectivity of cortical cells was found by single recording experiments (Hubel & Wiesel, 1962), these types of studies found a variety of bandwidths (De Valois et al., 1982b). The tuning range of cortical cells is most likely within the range of 15°-30°, which is in accordance with the masking and electrophysiological data, for the population of cells that are the most orientation selective (30%) (De Valois et al., 1982b).

1.2.6.4 Physiological and Anatomical Substrates of the Multiple Spatial Frequency Channels

Physiological studies also support evidence in favour of the existence of cortical multiple channels. The substantial binocular interaction or interocular transfer in terms of the specific consequences of spatial frequency adaptation (Blakemore & Sutton, 1969) also implies the involvement of a cortical area, because there is no such interaction at the earlier stages of visual processing (Wiesel & Hubel, 1966). Moreover, cells in the cortex are much more narrowly tuned to certain stimulus parameters, such as spatial frequency and orientation, as compared to cells in the LGN or in the retina (De Valois et al., 1982a; Maffei & Fiorentini, 1973; Maffei et al., 1973; Tootell et al., 1981) and there is a spectrum of cells sensitive to different bandwidths of these stimulus dimensions (Thorell et al., 1984). Simple and complex cells represent the first level in the geniculostriate pathway to show selectivity for narrow orientation ranges (Hubel & Wiesel, 1959, 1962). Single cell recordings from the monkey striate cortex show that most of the cells – both simple and complex – have narrow spatial frequency tuning of 1.4 octaves at half amplitude (the narrowest is 0.6 octave) (De Valois et al., 1982a; Movshon et al., 1978).

There is a general agreement between the psychophysical and physiological data in terms of the existence of multiple channels. The results for the bandwidths of the spatial frequency channels range between 1-1.4 octaves (De Valois & De Valois, 1988). The method of spatial summation implies very narrow, whereas masking experiments suggest broader tuning for example. One reason for this could be that different experimental designs might activate different processing mechanisms or different levels of processing. The other possible explanation is that some experimental paradigms postulate incorrect theories and consequently come up with misguided assumptions. It is also possible that different behavioural tasks activate cell populations to a different degree, therefore electrophysiological data is considered more accurate for these estimations.

1.2.7 Colour and Spatial Vision

Typically, the natural environment varies in terms of both luminance and colour at the same time therefore it is important to consider the spatial processing of colour defined stimuli. Colour information contributes to texture detection, visual search and object identification, based on the wavelength distribution of the light that is reflected by the surface. Contour detection is mostly carried out by the luminance detection system, but the chromatic differences also contribute to it, especially in cases when the chromatic contrast is very high (Geisler & Albrecht, 1995).

It is well known that processing of visual information takes place via three separate channels along the retino-geniculostriate pathway (Boynton, 1975; De Valois & De Valois, 1988) and it has been shown, that contrast sensitivity

functions for these three mechanisms are different. Colour contrast sensitivity was first quantified by Van der Horst & Bouman and Van der Horst et al. (van der Horst & Bouman, 1969; van der Horst et al., 1967), when they measured hue detection thresholds for isoluminant coloured gratings. They observed that at low spatial frequencies, perceived hue changes within the pattern in a regular continuous manner whereas gratings of high spatial frequencies are perceived as monochromatic luminance gratings, in which the colour component is the mixture of the two original colours of the grating and the other one is black. This might be an optical artefact or, as the authors suggested, pure chromatic detection, as long as the colours can be perceived, but higher spatial frequencies definitely result in luminance artefacts. Even though the tuning properties of cortical cells in case of luminance and colour patterns are approximately the same for both spatial frequency and orientation, there are small differences between the two mechanisms. CSF for colour in case where the grating is isoluminant and only contains colour differences remains steady in case of low spatial frequencies (up to 1 c/deg), but it shows a gradual increase at medium spatial frequencies (1-6 c/deg) and a marked decrease at high spatial frequencies (above 6 c/deg) (McKeefry et al., 2001; Mullen, 1985). Compared to luminance patterns, contrast sensitivity for chromatic gratings is higher at low spatial frequencies, but lower in case of high spatial frequencies (**Figure 1.18**) (Mullen, 1985). Consequently, the sensitivity of chromatic spatial vision is shifted towards lower spatial frequencies, and sensitivity is decreased at higher spatial frequencies. Luminance CSF is band-bass, while CSF for colour has low-pass characteristics at photopic levels. CSF for blue-yellow gratings begins to decrease at even lower spatial frequencies (Granger & Heurtley, 1973; van der Horst & Bouman, 1969). On the contrary, Mullen

(Mullen, 1985) reports that CSF for the two colour systems is the same. Overall, these differences between the colour and the luminance systems explain why the human visual system performs poorly when it comes to perceiving spatial details that are defined solely by colour.

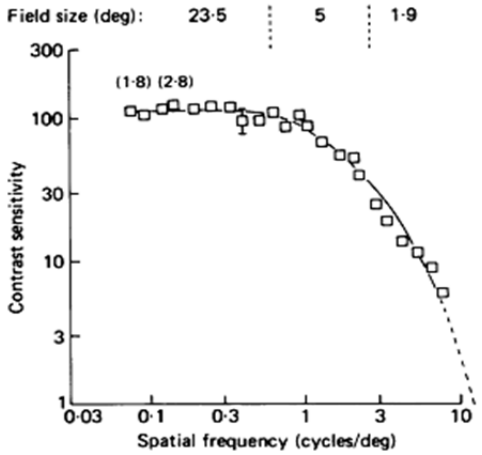


Figure 1.18 Illustration of contrast sensitivity as a function of spatial frequency, in case of a red-green grating. The figure illustrates that compared to luminance gratings (**Figure 1.15**), contrast sensitivity functions for chromatic gratings at low spatial frequencies are higher, whereas they are lower at high spatial frequency levels (Source: (Mullen, 1985)).

Chapter 2

Visual Short Term Memory

2.1 Introduction

This chapter provides an ovierview of memory with special emphasis on human visual short term memory. Human memory consists of a complex array of systems and processes, that enable us to store, retain and recall information about the environment and personal events (Fuster, 1997). Memory processes consist of three main stages; encoding, storage and retrieval. During encoding, sensory information is converted into a mental representation, which is retained in memory during the storage phase, and memory retrieval refers to the process when the stored information is actively accessed.

2.2 The Timescale of Memory

In terms of the length of time the information is stored for, we can distinguish between iconic, short term and long term memory (**Figure 2.1**). Iconic memory corresponds to the early stages of storage of sensory information, up until 500 ms after the display of the stimulus has terminated. It can be imagined as a very high precision, but quickly fading online representation of the visual image

(Sperling, 1960). Short term memory stores information for several seconds, or up to a few minutes, depending on the task, and has limited capacity. It mostly serves as a temporary storage during the time a person carries out a certain behavioural task and is a substrate for the formation of long term representations (Atkinson & Shiffrin, 1968). Long term memory is formed through rehearsal and meaningful associations of the information stored in short term memory. It is able to store a great amount of information for infinite amount of time (**Figure 2.1**) (Magnussen et al., 2003). There are two distinct long term memory processes; explicit, or declarative memory stores conscious information about facts and events and consists of episodic and semantic memory (**Figure 2.2**) (Tulving, 1972). Episodic memory stores information about individual experiences in life, such as events, times, places, associated emotions, contextual knowledge and serves as an autobiographical reference. Semantic memory stores factual information and general knowledge, understanding of the world and other concept-based knowledge, which are not related to individual experience. It is less susceptible to unintentional loss, or modification of information due to new information or retrieval, compared to episodic memory. The other type of long term mechanism, named as implicit, or procedural memory stores information about skills (i.e. how to do things), and it is considered be an unconscious form of memory (**Figure 2.2**).

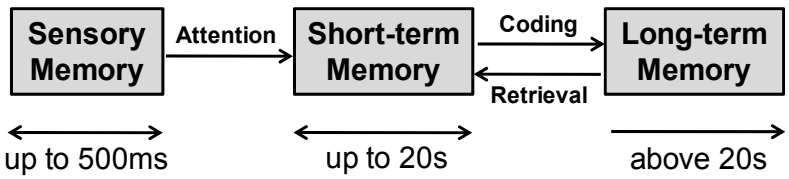


Figure 2.1 Timescale of memory processes. See detailed explanation in text.

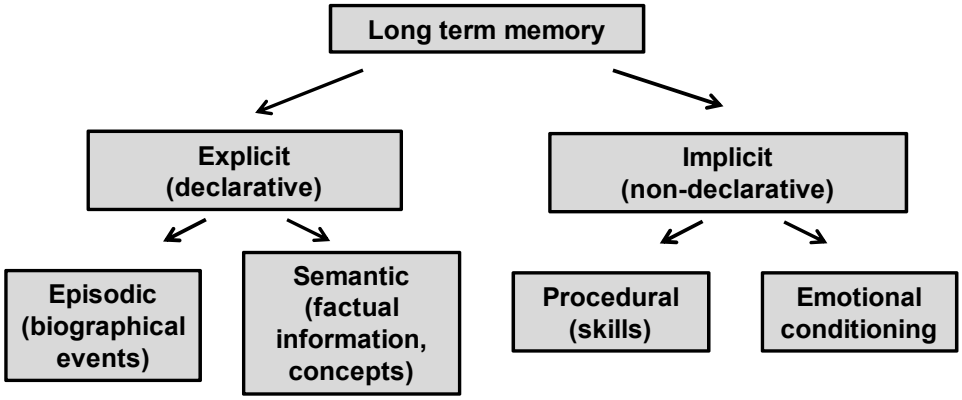


Figure 2.2 Classification of long term memory systems. See detailed explanation in text.

2.3 Memory Models

There are various behavioural models of memory in the literature, which attempt to represent and describe memory mechanisms (Atkinson & Shiffrin, 1968; Baddeley, 1983; Broadbent, 1958; Craik & Lockhart, 1972).

Broadbent (Broadbent, 1958) proposed the 'Modal model', according to which there are two separate small short term memory systems that work in a parallel manner and project into a limited capacity storage system that feeds automatically into long term memory (**Figure 2.3**). The perceptually processed information in the short term store is filtered for further processing before it is transferred via the limited capacity channel to the 'system for varying output until some input is secured' and the 'store of conditional probabilities of past events' (**Figure 2.3**). Feedback mechanisms also operate and modulate this system. However, it proved to be difficult to explain the wide range of experimental results using this model.

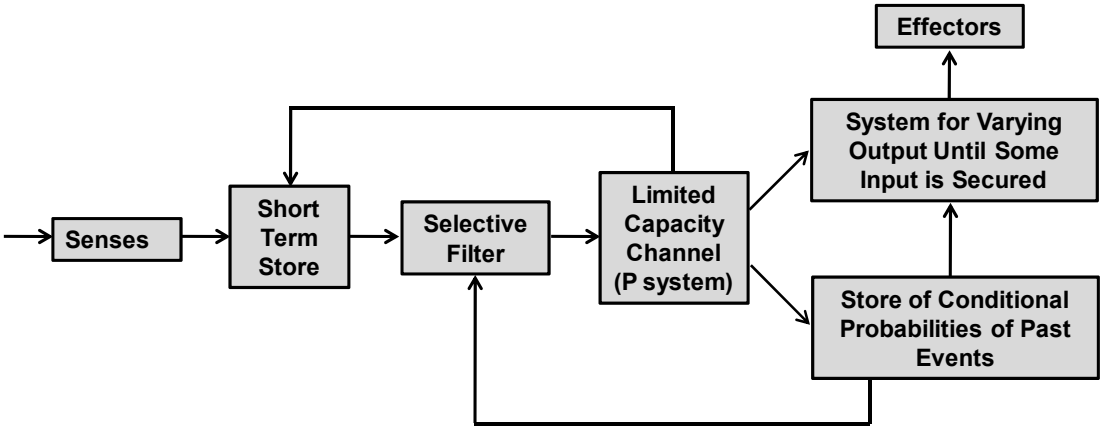


Figure 2.3 Illustration of the Modal model of Broadbent (Broadbent, 1958). See explanation in text.

Later on the Atkinson-Shiffrin model was developed (Atkinson & Shiffrin, 1968), which is very similar to the theory of Broadbent (Broadbent, 1958). This model describes three types of memory store; sensory store, short-term store and long term store (**Figure 2.4**). According to this model, sensory information is analysed via parallel mechanisms in the sensory storage, which has a limited storage capacity and conveys incoming information into a short term storage system, where information is retained for up to a few minutes (**Figure 2.4**). The storage of information in this short term storage is easily accessible, but is very fragile, it can easily be overwritten by subsequent stimulus presentations and it serves mostly as a basis of the formation of long term memory representations. Short term memory in this model has a central importance in terms of storing information and monitoring memory formation. Increases in the rehearsal time increase the likelihood that an information will be stored in long term memory.

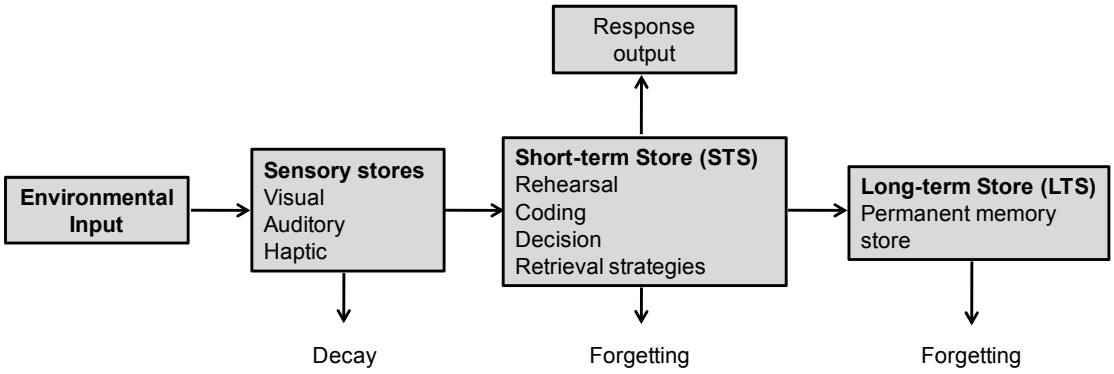


Figure 2.4 Illustration of the Atkinson and Shiffrin memory model. See explanation in text (Atkinson & Shiffrin, 1968).

Craik and Lockhart (Craik & Lockhart, 1972) placed more emphasis on the mode and depth of processing instead of the structures that take part in the processes, hence the name of the model 'levels of processing'. The durability of the memorized item depends on the depths and type of processing of the memorandum. 'Shallow processing', such as maintenance rehearsal and less accurate recall involves elaboration based on appearance of the stimulus, and it is a short lived representation, whereas 'deep, or thorough' processing, which is based on semantic processing and more rehearsal leads to a better memory representation and more accurate recall. According to this model, the major role of the primary memory system is to deal with the analysis of the information that reaches the system.

2.4 Cortical Substrates of Memory

The two most important cortical loci of memory, which are responsible for both short and long term storage, are the sensory and the frontal areas of the cortex. Evidence concerning the roles of these areas comes from electrophysiological and lesion studies, which initially attempted to attribute distinct cognitive memory functions to circumscribed cortical areas (Fuster, 1997). Recent literature demonstrates that most of the areas that are responsible for the

storage of information are located in the neocortex, and work together as a network of interconnected locations (Fuster, 1997). This notion has been widely accepted, and recent physiological and neuroimaging studies have been conducted to further explore this organisational principle (Jonides et al., 1993; Petrides et al., 1993; Swartz et al., 1995). Subcortical areas also take part in memory formation; the hippocampus has a crucial role in the development of memory networks for individual and long term memories, whereas the amygdala, located in the temporal lobe, assesses emotional and affective consequences of perceptions, and takes part in the shaping and consolidation of memories (Fuster, 1997).

2.5 Short Term Memory

2.5.1 Model of Working Memory

Working memory refers to a complex neural system that serves as a temporary storage of information during the time an individual carries out a behavioural task, such as learning or remembering a phone number (Baddeley, 1986). It can also be imagined as a mental sketchpad, which works on the basis of retrieval and utilization of the recently acquired knowledge, a mechanism that is distinct from the mechanisms of long term memory and learning (Baddeley, 1986).

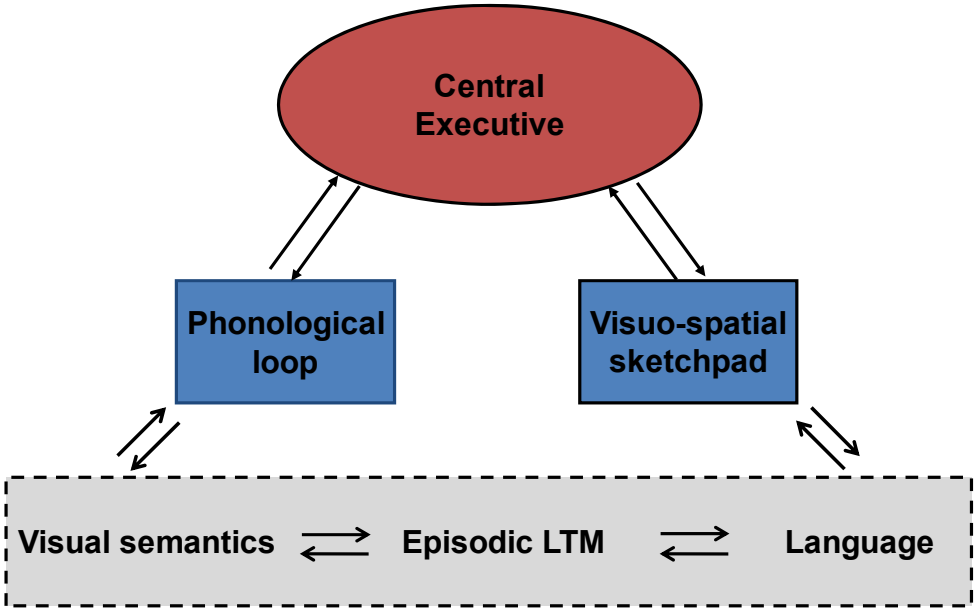


Figure 2.5 Baddeley's model of working memory (Baddeley, 1983). See detailed explanation in the text. The model was later modified as indicated by the box in the dashed line. These additional cognitive processes emphasize the role of language in the working memory processes, learning, and the build-up of long term representations (Baddeley, 2000).

Based on experimental results Baddeley (Baddeley, 1983) introduced the term working memory, which is a more complex concept than the STM system. The performance of the observers was measured in a dual task, where, their short term memory performance was disturbed by having to rehearse a sequence, while they executed a behavioural task. Based on the results, Baddeley constructed a working memory model (**Figure 2.5**), which consists of three main components; the central executive (CE), the articulatory, or phonological loop and the visuospatial sketchpad (VSSP). The central executive acts as a limited capacity attentional control system (i.e. it runs and chooses control processes and strategies), which oversees and modifies the work of its two main slave subsystems (**Figure 2.5**). The articulatory or phonological loop is responsible for the speech coding and maintaining of linguistic information by subvocal rehearsal. The existence of this system explains several experimental phenomena, such as the phonological similarity effect, the word length effect, the unattended speech effect and the articulatory suppression effect (Baddeley

et al., 1998; Baddeley et al., 1975). The visuo-spatial sketchpad carries out the temporary storage and manipulation of visuospatial information. This system receives information either through perception, or indirectly via visual imagery. The active mechanisms taking place in these two subsystems can be easily disrupted by simultaneous stimuli or activities. The operation of the CE is overseen by the Supervisory Attentional System (SAS), the role of which is to override habits to enable new achievements in response to the environmental circumstances. The model was later on complemented with further cognitive processes that are meant to support the build-up of long term representations in memory (see **Figure 2.5**) (Baddeley, 2000). According to this modified model, there is a fourth component of WM, the episodic buffer, which integrates information coming from the slave systems (**Figure 2.5**). It uses previous knowledge to process information more effectively (Baddeley, 1983, 2000).

2.5.2 Cortical Substrates of Human Visual Short Term Memory

As mentioned earlier, in the human brain, sensory and memory areas work together in a network in VSTM (Visual Short Term Memory), within which the different areas possibly have the same organisational features (**Figure 2.6**) (Courtney et al., 1997; Pasternak & Greenlee, 2005).

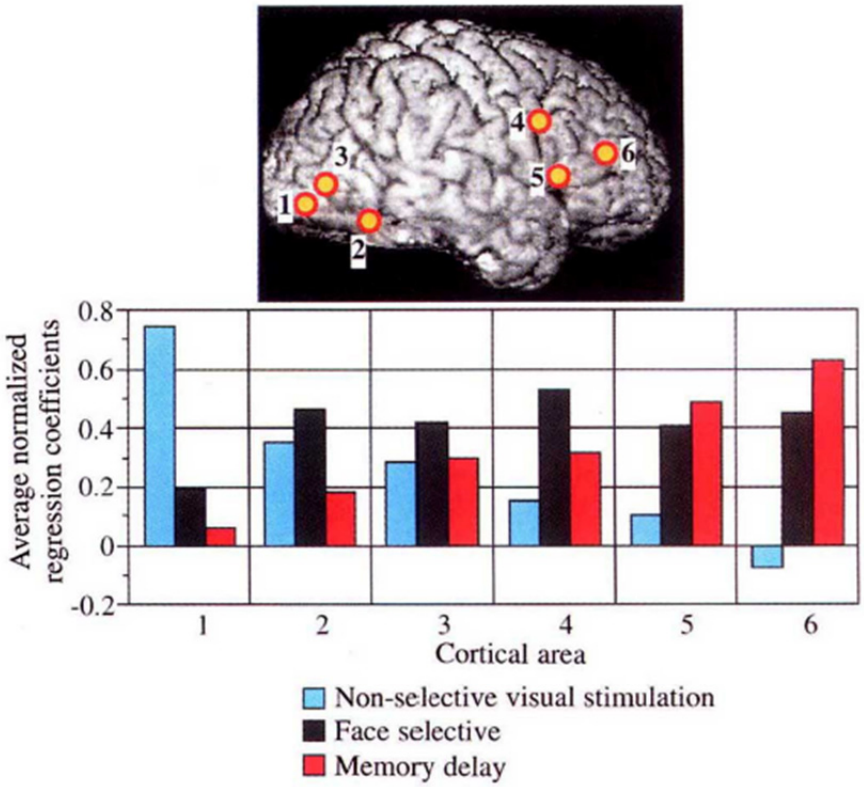


Figure 2.6 Illustration of network memory for short term processes in the human brain. The figure shows averaged locations across subjects of the activated areas on the right hemisphere in a short term memory task for faces. The activated regions are the following: 1) Posterior lingual and fusiform gyri, 2) mid-to-anterior fusiform gyrus, 3) inferior occipital sulcus, 4) posterior mid- and inferior frontal gyri, 5) inferior frontal gyrus and anterior insula and 6) anterior mid-frontal gyrus. The figure illustrates the existence of a network that consists of brain areas distributed throughout the cortex, located beyond V1 in the cortical processing stream. This network has a dual function involving the sensory encoding and short term storage of information (Source: (Courtney et al., 1997)).

Studies have shown that the Prefrontal Cortex (PFC) (**Figure 2.7**) integrates information to guide complex behaviour, it has a role in a number of mechanisms, such as attention, response selection, planning, inhibitory control, integration and learning associations, and exhibits stimulus related activity during memory tasks, especially in short term memory (Fuster, 2000; Goldman-Rakic, 1995; Miller, 2000). The PFC enables the individual to focus his/her attention on a given sensory input, thought or action, in other words, selects the behaviourally important information, which is crucial due to the limited capacity of higher order cognitive functions. It is responsible for planning and executing complex goal directed actions (Miller, 1999). Additionally, it is thought to have a

major role in learning new goal directed behaviours and associations (Miller, 2000). The prefrontal cortex (PFC) has a major role in working memory (Goldman-Rakic, 1987), and it is also responsible for recollecting previously stored information in view of the recent events (Watanabe, 1996). It seems that PFC has an executive role in top down processing in memory, namely, the Inferior Temporal cortex (IT) is activated by the PFC during memory retrieval (Tomita et al., 1999).

Electrophysiological studies on awake monkeys have made a major contribution to our present knowledge about the PFC (Fuster & Alexander, 1971). These studies have shown enhanced activity of PFC neurons during delayed discrimination experiments (Fuster & Alexander, 1971). Activation patterns of neurons in the principal sulcus of PFC include phasic activation in response to visual stimuli, tonic activation during the delay, and phasic reactivation before the response (Fuster & Alexander, 1971). It has also been hypothesised that the PFC is organized in terms of cortical columns, where, within the laminar structure each column is devoted to a certain memorandum. Areas responsible for storing visuospatial information are separated from areas coding simple, complex or categorical attributes. Different neurons respond to different stimulus features (Wilson et al., 1993) and to different stimulus locations (Funahashi et al., 1989). Moreover, the neurons in PFC that are tuned to different object locations have opponent characteristics, meaning that while one neuron is maximally active in one object location, its firing is inhibited when the stimulus is presented in a different location (Funahashi et al., 1989). Memory fields are constructed on the principle of horizontal interactions and vertical feed-forward inhibition, and pyramidal-nonpyramidal interactions play a crucial role in the build-up of memory fields (Goldman-Rakic, 1995). Neurons in the

inferotemporal (IT) and parietal cortex also show memory related activity during the delay period while information about objects and complex shapes is retained (Fuster, 1990; Miller et al., 1993; Miyashita & Chang, 1988).

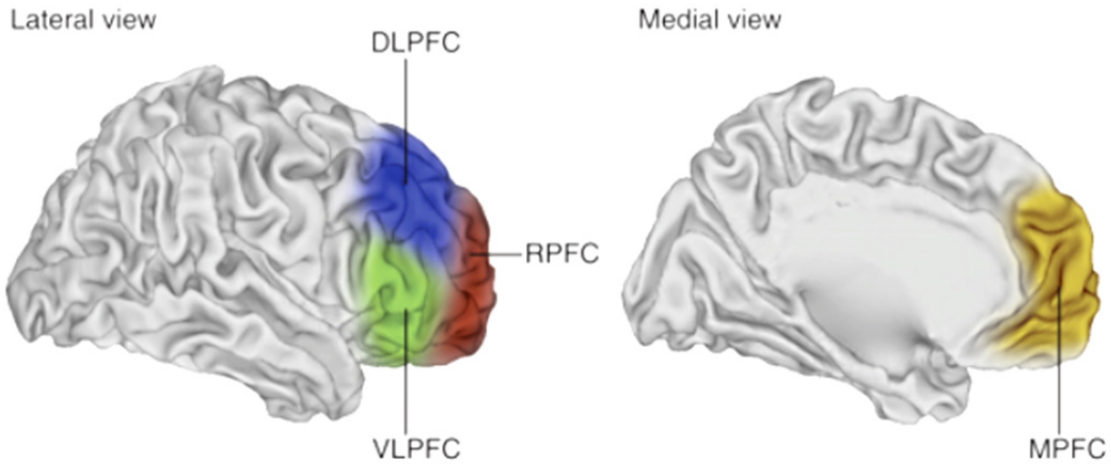


Figure 2.7 Illustration of the Prefrontal Cortex (PFC). The PFC is known to have a major role in memory networks. See detailed explanation in the text.
(Bownd D. (29 Feb 2008) [Online Image]
Available at: <http://mindblog.dericbownds.net/2008_02_01_archive.html> [Accessed 23 August 2010]).

FMRI (Functional Magnetic Resonance Imaging) is a valuable tool for the investigation of memory networks, and can help in the identification of brain areas that take part in specific memory tasks (**Figures 2.6** and **2.7**). However, activation patterns appear to depend on the type of experimental technique used. Studies that have employed n-back tasks tend to find substantial neuronal activity outside the sensory cortex (Courtney et al., 1997), whereas studies employing delayed discrimination tasks tend to identify activity in the occipital cortex, as well as in temporal and parietal areas (Greenlee et al., 2000; Pessoa et al., 2002). This finding suggests that different tasks exploit different combinations of cortical areas. However, there is an agreement that spatial storage tasks evoke an fMRI signal in the superior parietal cortex, whereas memory for objects is located in the inferior temporal cortex, as well as in the parietal cortex (Pessoa et al., 2002).

A comprehensive analysis of neuroimaging studies found a dorsal-ventral dissociation in posterior parietal cortex between different types of stored information, such as verbal (i.e. words, letters, linguistically coded information), spatial (spatial position of stimuli) and object information (non-spatial visual features, object identity) (Wager & Smith, 2003). The dorsal pathway is responsible for the processing of spatial information, and projects from the extrastriate cortex towards the inferior parietal lobe and intraparietal sulcus in a feed-forward manner. The ventral stream carries out analysis of object information, and it comprises projections from the extrastriate cortex to the inferior surface of the frontal lobe (D'Esposito et al., 1998; Mishkin & Ungerleider, 1982; Smith & Jonides, 1998; Wilson et al., 1993). D'Esposito et al. (D'Esposito et al., 1998) examined the organization of neurons based on the type of information processed with event related fMRI, and found dorsal-ventral dissociation in the PFC as well. Ventral PFC receives information from posterior association areas (active comparison of information), and has a role in rehearsal during simple storage mechanisms, whereas dorsal PFC is involved in monitoring and manipulating information in working memory. There might also be a hierarchical organization of the information transmitted from ventral to dorsal cortex (D'Esposito et al., 1998).

2.5.3 Visual Attributes of Perceptual Short Term Memory

Memories that are realized through the sensory modalities belong to perceptual memory, which includes all individual memories and knowledge of personal information, such as events, objects, persons, animals, facts, names and concepts. These areas are hierarchically organised, and a separate array of systems belong to each of the three sensory modalities; vision, touch and

audition (Fuster, 1997). Visual Short Term Memory is a type of short term memory, which is involved in the processing and storage of visual stimuli.

Evidence for feature specificity in visual perceptual memory has emerged from psychophysical studies. In many cases, these have employed delayed discrimination paradigms, where the ability to retain information about basic stimulus attributes was measured over a time delay or inter-stimulus interval (ISI) (**Figure 2.8**) (Regan, 1985). The quality or fidelity of the retained information can then be indexed by changes in performance. Using this approach, the retention of different stimulus features (contrast, orientation, spatial frequency, vernier offset etc.) was found to have different rates of decay with increasing ISI, which suggests that different perceptual memory mechanisms exist for different attributes (Fahle & Harris, 1992; Lee & Harris, 1996; Magnussen & Greenlee, 1999; Magnussen et al., 1996; Magnussen et al., 1998; Vogels & Orban, 1986).

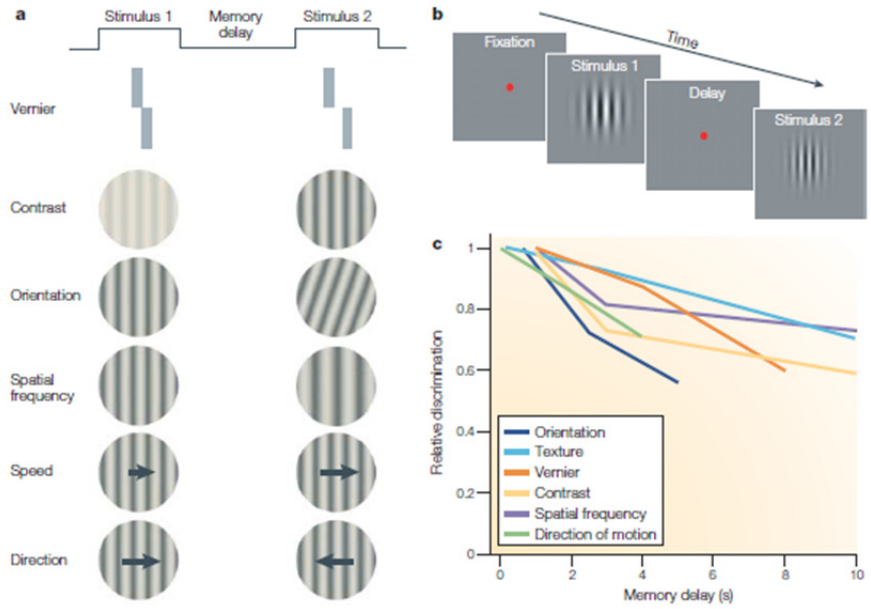


Figure 2.8 Visual working memory for visual stimulus dimensions. A delayed discrimination paradigm is illustrated in Figure a), with representative examples of visual stimuli that are employed in order to investigate the retention characteristics of these stimulus attributes. Section b) illustrates the results of these delayed matching experiments, which indicate a high accuracy for the retention of basic visual attributes for up to 10 s ISIs (Source: (Pasternak & Greenlee, 2005)).

2.5.4 Organisation of VSTM

Current research in perceptual memory has focussed on the different attributes of stimuli which are processed by the visual cortex (Magnussen, 2000; Woodman et al., 2003). Psychophysical studies on VSTM have traditionally employed delayed discrimination paradigms to examine performance for elemental stimulus dimensions, such as orientation, contrast, velocity, spatial frequency and colour, and the individual's performance has been assessed on the basis of discrimination thresholds (**Figure 2.8**) (Magnussen & Greenlee, 1992, 1999; Magnussen et al., 1990; Magnussen et al., 1991; Magnussen et al., 1998). During this kind of experimental design, reference and test stimulus presentations are temporally separated by a 1-30 s interval and the observer has to make a decision as to whether the test has the same or different properties compared to the reference with regards to a particular dimension. The advantage of these tasks is that the response is dependent solely on the previously presented stimulus, and the correct response cannot be anticipated from previous stimulus presentations, therefore a new decision has to made on every single trial. These studies have revealed that VSTM consists of individual parallel mechanisms, which are connected with separate storage systems, but linked by a lateral inhibitory network. Each of these pathways processes information about a single characteristic of the visual stimulus, such as contrast, velocity, spatial frequency, orientation and colour. The experiments have furthermore shown that there is a high degree of accuracy in working memory for spatial frequency, velocity, motion (Greenlee et al., 1995; Magnussen & Greenlee, 1992; Magnussen et al., 1991) and for orientation, up until 30 s (Magnussen et al., 1985). There is a slightly decreasing accuracy with time delay for contrast (Greenlee et al., 1991b) and colour (Nilsson & Nelson, 1981).

According to Magnussen (Magnussen, 2009), representations of visual stimuli in visual short term memory belong to the system of implicit memory. Implicit memory conveys information to the perceptual representation system (PRS), which is responsible for identifying objects based on perception, and might serve as the basis of forming long term memories. One piece of evidence that supports this notion, is that even though observers can only describe stimulus differences within a dimension in a coarse way, their performance is extremely accurate in delayed discrimination tasks. There is an increase in the reaction times that observers need in order to respond as the duration of the interval is increased, during which a certain stimulus has to be retained in memory. This denotes a shift from perceptual representations (3-4 s) to storage mechanisms (Magnussen et al., 1998). Once a memorandum is stored, more time is required for the response, because the information has to be retrieved from the memory store in order to be readily available during the task. However, this does not seem to result in any change in discrimination thresholds during delayed matching tasks (**Figure 2.8**) (Magnussen, 2000).

2.5.5 Cortical Locus for VSTM

The cortical network of VSTM is believed to be located beyond the primary visual cortex (V1) but early in cortical processing (Magnussen, 2000, 2009; Magnussen & Greenlee, 1999). The anatomical areas that are involved in this process are still in the focus of research, but there is a general agreement that occipitotemporal, frontal, prefrontal, parietal cortex, anterior cingulate and basal ganglia are essential parts of this functional system. The perceptual areas that process these stimulus attributes are undoubtedly involved in the memory processes and work together as a network.

Haxby and colleagues examined the multiple regions of the brain that have a functional role and work together as a network in VSTM (Haxby et al., 2000). Haxby et al. developed a task in order to be able to differentiate between sustained memory maintenance activity and transient perceptual activity, as well as motor activity. During the experimental scanning sessions subjects performed spatial and face memory tasks, and the different regions were identified on the basis of the amount and manner of their relative activation during stimulus presentation (transient activation) and memory delays (sustained activity). The timescale of the activations, as well as active regions in the temporal and parietal extrastriate regions were also examined, and six regions in the frontal lobe were identified which showed significant activation during the task. The scale of activation of these regions in relation to each other was found to be different for different tasks, such as spatial or face memory, and during the perceptual and memory phase. The more anterior regions showed stronger memory maintenance related activity, and three prefrontal regions; inferior frontal gyrus, posterior middle frontal gyrus, anterior middle frontal gyrus exerted high activity during memory delays and a transient reaction to face stimuli. PFC activated regardless of the memory task that was carried out.

In order to test the sensory recruitment hypothesis, namely, whether sensory areas take part in the activation patterns during VSTM in a stimulus specific manner, Serences et al. focused on V1 that processes both orientation and colour at a sensory level (**Figure 2.9**) (Serences et al., 2009). Memorandi were gratings of different orientation, or coloured Gabor patches, which had to be retained over a 10 s ISI in a two-alternative forced choice task. Multi-voxel pattern analysis (MVPA) showed that sensory regions activate in response to

certain specific stimulus attributes, representing storage specific activation (**Figure 2.9**).

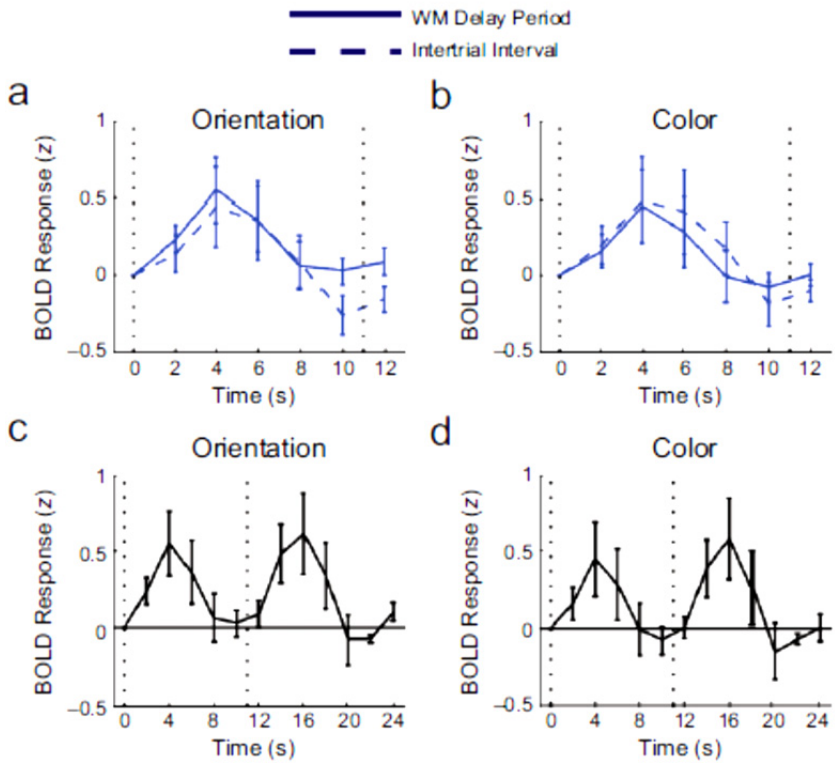


Figure 2.9 Mean amplitudes of the blood-oxygenation-level-dependent (BOLD) signals in primary visual cortex (V1) during memory delays (ISI) and inter-trial intervals (ITI). The vertical dotted lines indicate the onset of the reference and test stimuli at 0 s and 11 s, respectively. Graph a) illustrates results for orientation and b) for colour tasks over a time frame that continues 12 s after the stimulus appearance, and the graphs at the bottom show results for c) orientation and d) colour memory tasks over a longer, 24 s long temporal window (Source: (Serences et al., 2009)).

In a different fMRI experiment, observers performed a delayed discrimination task, where the orientation of the grating had to be remembered (**Figure 2.10**) (Harrison & Tong, 2009). The aim was to examine whether the pattern of the activation within the sensory regions would predict the orientation of the grating, since V1-V4 regions show an orientation selective activation pattern. By employing pattern classification methods (population decoding method), they showed stimulus dimension specific activation in V1-V4. Moreover, based upon the activation patterns of these early visual areas, Harrison and Tong were able to infer what orientation the grating had (i.e. in what sort of stimulus dimension

the stimuli differed), and this increased activity was present throughout the delay periods (Harrison & Tong, 2009).

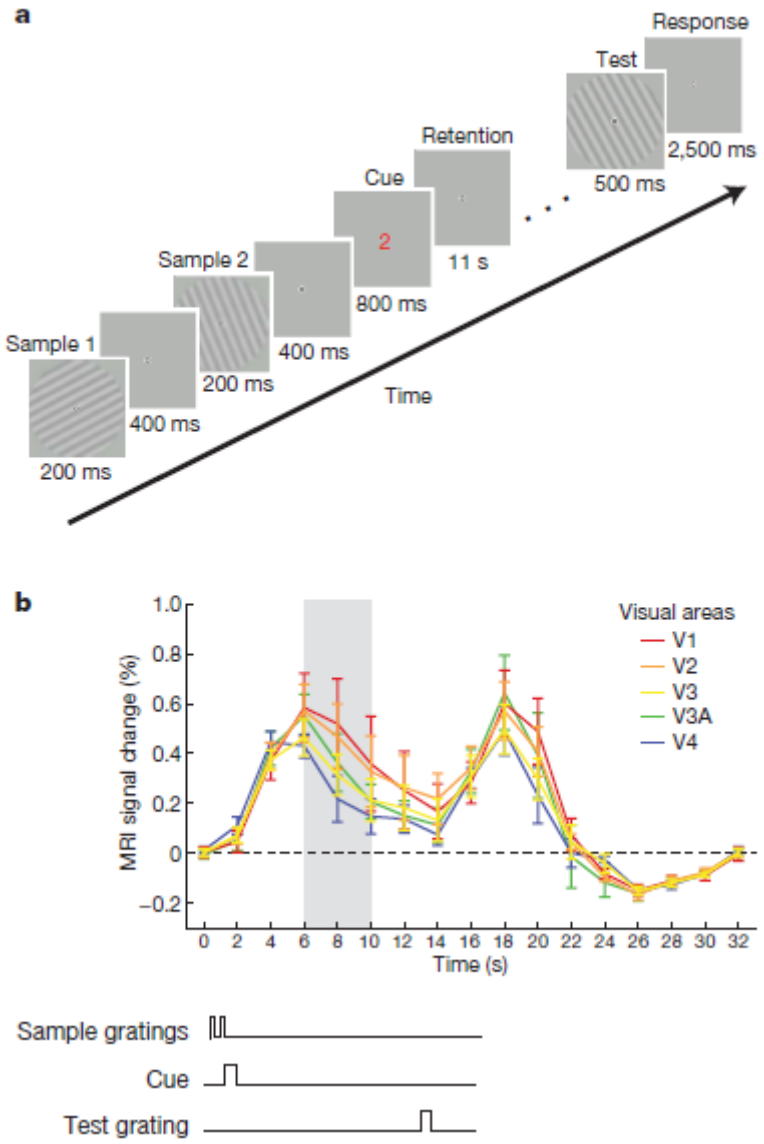


Figure 2.10 A visual working memory experiment and time course of fMRI activity in visual areas. Figure a) shows the timing of events for a working memory task. Two near-orthogonal gratings were presented in randomized order, and the observer was cued with numbers, which grating to remember. A test grating was displayed at the end of the 11 s time delay, and subjects were asked to indicate the direction of its rotation compared to the cued grating. Figure b) shows the time course of the BOLD activity in areas V1–V4 during task (between 0–16 s) and the following fixation period (between 16–32 s) (Source: (Harrison & Tong, 2009)).

Offen et al. (Offen et al., 2009) performed experiments, where in each of the different runs the same visual stimuli were presented, but the tasks loaded memory and required attention to a different extent. Different delays were

employed, and the tasks were carried out close to threshold levels of performance. Delayed comparison tasks, detection tasks, cued detection tasks and discrimination tasks were employed. Predominantly memory and predominantly attention tasks evoked different activity patterns, early visual cortex was more activated during increased attention demands, and this effect was most prominent in V2, V3, LO1, LO2, and less robust but present in V1, V4 and V3A/B.

In a recent study by Sneve et al. (Sneve et al., 2011), BOLD activity in V1 was measured while subjects carried out a delayed match-to-sample task employing memory masks of varying spatial frequencies. They found weaker activity in V1 while performance was impaired by the mask stimuli. This finding explains the discrepancy between studies that employed univariate analyses as opposed to MVPA (Multi Voxel Pattern Analysis) when exploring the role of V1 in VSTM mechanisms (Harrison & Tong, 2009; Offen et al., 2009; Serences et al., 2009). According to the model they formulated, the areas which take part in the retention of visual information show a weaker response during the memory masking paradigm, due to a lateral inhibition effect which results in the inhibition of neurons that are not responsive to the actual stimulus and consequently an overall weakening of the BOLD signal. This finding serves as further evidence for the existence of multiple channels and cross channel interaction in VSTM for spatial frequency.

2.6 Psychophysical Studies Examining the Modular Nature of VSTM

As mentioned before, in a typical visual working memory task in psychophysics, a delayed discrimination paradigm is employed. In this kind of task, participants

compare differences between stimuli in a given stimulus dimension and make same-different judgments. The effect of time delay and further interfering factors are assessed in terms of the discrimination thresholds, which reflect the precision with which stimulus information is retained, as well as in terms of perceived shifts in the examined stimulus dimension.

The short term storage of visual information has not only been studied at single neuronal levels as well as with behavioural methods (Bisley et al., 2004; Fuster, 1990). These studies have indicated that VSTM consists of individual parallel mechanisms of high fidelity, which are connected with separate storage mechanisms, and each of the pathways processes information about a single characteristic of the visual stimulus, such as contrast, orientation, spatial frequency, speed and direction. Studies that examined discrimination thresholds for the different visual stimulus dimensions showed a very high accuracy with almost no decay for inter-stimulus intervals of up to 30 s for orientation (Magnussen & Greenlee, 1992; Magnussen et al., 1990; Magnussen et al., 1991; Magnussen et al., 1998; Nilsson & Nelson, 1981; Pasternak & Zaksas, 2003).

2.6.1 Memory Masking

In order to examine the dimension specificity of VSTM, typically a memory masking paradigm is employed. Performance of a delayed discrimination task can be disrupted by the introduction of a masking stimulus during the ISI, which results in elevated discrimination thresholds (**Figure 2.11**) (Magnussen & Greenlee, 1992; Magnussen et al., 1991; Pasternak & Greenlee, 2005). The use of this so called ‘memory mask paradigm’ verified previous assumptions that the stimulus attributes within working memory are separately processed

(Magnussen, 2000; Magnussen & Greenlee, 1999; Magnussen et al., 1996; Magnussen et al., 1998). Memory masking increases discrimination thresholds when the mask has different properties to the reference within the examined stimulus dimension. For example, if spatial frequency and orientation of a grating are assessed simultaneously, then a memory mask of different spatial frequency will interfere with spatial frequency discrimination ability only, and discrimination thresholds for orientation will be intact. It is thought that this effect occurs because the different dimensions are processed via independent mechanisms, but these mechanisms can possibly interfere with each other during the rehearsal process (Magnussen & Greenlee, 1992). The fact that the masking effect only occurs when there is a change within the same stimulus dimension supports the existence of the inhibitory network and the narrow tuning assumptions of the model. The dissociation between different stimulus attributes when memory masking is employed implies that these mechanisms take place beyond V1, at a location where they are separately processed (Magnussen, 2009; Magnussen & Greenlee, 1999).

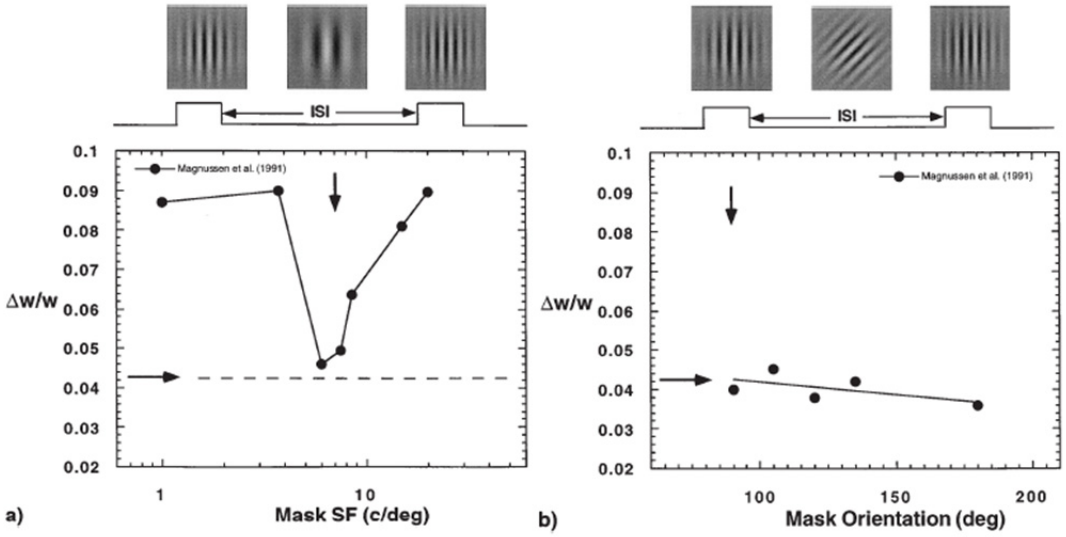


Figure 2.11 The effect of a mask grating presented in the middle of a 10 s long ISI in a delayed match-to-sample paradigm. These graphs show discrimination thresholds expressed as Weber fractions, and plotted as a function of a) mask spatial frequency and b) mask orientation. Baseline performance is indicated by the horizontal lines and refers to a condition, where no mask was presented. The plots show, that when the mask has a very different spatial frequency from the reference, it is capable of disrupting the performance, whereas if they are similar, the discrimination thresholds remain similar to that of the baseline. In case a different visual dimension is introduced, such as orientation, no interfere is evoked which is indicated by the lack of change in the discrimination thresholds as a function of mask orientation. These results support the idea that they are processed via separate channels (Source: (Magnussen & Greenlee, 1999)).

2.6.2 Memory for Colour

The major focus of this thesis is VSTM for colour, therefore I include a detailed review of the available literature in this section. In everyday life, colour is regularly used as an aid to search for, and recognize objects in the environment. There are various situations, when we are required to compare a colour with a previously remembered one, performing successive colour matching. There is a vast amount of literature, which examined colour memory for various time delays, examining sensory memory, short term memory, and long term memory and for the fundamental attributes of colour, such as hue, saturation and brightness. Even though different approaches were used, which makes the comparison of the results difficult, there has been a general agreement in most of these studies, namely, that colours stored in memory are

different from the originally presented stimuli. Shifts in hue, due to degradations in VSTM, are minor and do not represent a consistent direction (Bartleson, 1960; Burnham & Clark, 1955; Collins, 1932; Hamwi & Landis, 1955; Loftus, 1977; Newhall et al., 1957; Nilsson & Nelson, 1981; Perez-Carpinell et al., 1998). Saturation tends to shift towards a more saturated appearance in most of the cases (Bartleson, 1960; Burnham & Clark, 1954; Burnham & Clark, 1955; Newhall et al., 1957; Siple & Springer, 1983), and shifts in brightness have a tendency to be dependent on the luminosity of the original stimulus; bright colours are remembered as even brighter, and darker stimuli are remembered as being darker and more saturated.

There are various factors that influence the results of colour memory experiments, such as previous experience, the usage of colour terms, the type of task or experimental design that is employed, selection of remembered colours out of coloured swatches, adjustment tasks or delayed matching tasks. The accuracy of the storage process is also influenced by the focality, or saliency of colour, these colours are usually the most saturated in a colour category, and they tend to be remembered more accurately (Heider, 1972). As a result of a regular contact with them, the typical colours of known objects are also well retained in memory (Ratner & McCarthy, 1990). Adaptation to a specific colour can also influence further perception and result in specific hue, saturation and brightness shifts from the actual colours (Newhall et al., 1957). The context in which a certain colour is presented also has an impact on colour memory (Francis & Irwin, 1998), colourful or contextual surrounding facilitates a more accurate storage of colour information in memory. On the whole, there seems to be a tendency for colours to shift in the direction of a more salient

representation, that is, brighter or darker, more saturated or towards a focal colour.

This literature review is organised by devoting separate sections to the three attributes of colour; hue, saturation and brightness. The most explored attribute is hue, and the fact that the results are the least consistent in this case demonstrates the extent to which the time delay, stimulus configuration, matching paradigm and subjective factors affect the results. Experiments for short and long term memory are reported jointly.

2.6.2.1 Colour Memory and Hue Shifts

One of the first studies to examine if there were any differences in the accuracy of remembering different colours was carried out by Collins (Collins, 1932). Four basic colours (red, green, blue and yellow) were presented using a spectrometer, simultaneously, and after a 15 s delay. A patch of random colour, different from the remembered one appeared, and observers had to adjust the spectroscope until it matched the original one. Despite large individual differences and observed learning effects, the results showed that yellow and blue were remembered most accurately, red and green were more difficult to retain, and there was a much greater variability of the matches in case of these two colours, with the matched colour being shifted away from the original one. There were no shifts of uniform direction, it was therefore concluded that the overall ability to retain colours of different wavelengths are diverse along the spectrum.

Inspired by the fact that there was a lack of standard tests that enabled comparable experiments to investigate immediate colour memory, a test was built by Burnham & Clark (Burnham & Clark, 1954; Burnham & Clark, 1955),

which served as a baseline for many subsequent studies and test developments. In total, 43 different hues of the Farnsworth-Munsell hue series, equal in saturation and brightness were exploited, spaced equally around a circle. There was an inner circle for reference memory colours, containing 20 values, and the remembered colour had to be chosen from the 43 chips of the outer circle after a 5 s delay. There was a high variability of the matches and hue shifts were found in case of greenish yellow (towards reddish yellow), bluish green (towards bluer green), reddish blue (towards blue) and bluish red (towards a bluer bluish red) but there were no consistent directions when testing colour memory under these conditions. One advantage of this test is that accuracy is not better in case of experienced observers, therefore this particular short term memory test is not influenced by training. Based on earlier reports on colour memory (Burnham & Clark, 1955; Collins, 1932; Newhall et al., 1957), an experiment was performed by Newhall et al. (Newhall et al., 1957), in order to compare differences between simultaneous and successive colour matching in terms of principal characteristics such as hue, saturation and brightness. Twenty-five different test colour patches were presented in simultaneous and successive matching tasks, which employed a 5 s delay, and performance was compared. The introduction of the time delay resulted in a significantly higher variability of the hues and shorter response times, and pure colours were remembered more accurately. Matched colours were of higher saturation and brighter than the original ones. It was assumed that one explanation for this phenomenon was that the eye adapted to colours during the experiments, therefore observers needed stronger stimuli to evoke the same ‘perceptual’ effect. This raises concerns and denotes that caution has to be exercised when drawing conclusions based on a certain experimental paradigm. Accuracy,

discrimination ability and influences on the colour memory process were assessed by Perez-Carpinell et al. (Perez-Carpinell et al., 1998), investigating colour memory on a larger number of observers (n = 50). Ten different colours were used as references and observers had to choose the remembered colour from 20 samples simultaneously, and after 15 s, 15 min and 24 hr delays to estimate to what extent these time delays influence the accuracy of colour memory. Simultaneous matching resulted in high accuracy, whereas performance significantly decreased and colour discrimination showed a greater variability with increasing time delay. Subjects generally selected lighter colour chips, and the greatest variability was found for yellow, light green, blue and pink, whereas orange was remembered the most correctly. A series of experiments were performed by de Fez et al. (de Fez et al., 2001), to demonstrate the effect of memory on the appearance of certain colours. Reference colours were 34 Munsell chips of the four main hues such as yellow, green, purplish-blue and reddish-purple. In case of each colour, a significantly more salient version was remembered after a 10 min delay, but there was no definite arrangement of shifts among the hues and in terms of brightness. However, there was a tendency of the most accurately matched colours to be located along the red-green perceptual axis, and the least along the blue-yellow one.

Two different sets of experiments were performed by Hamwi & Landis (Hamwi & Landis, 1955) with the intention to examine whether time delay or the complexity of the task causes a greater variability of the remembered colour. In the so-called ‘unmixed design’, 672 Munsell colour chips were arranged in an orderly fashion and the memorized colours (10 different chips) were selected by the observers after 15 minute, one day and one week delays. During the ‘mixed

condition' experiments, the difficulty was increased by presenting 169 colour chips including the test colour, in a random order at the same time, after which the memory tasks were performed with the different time delays. Accuracy significantly decreased after 15 min and further delays did not further impair the performance. Blue-green and red-purple colours were the most difficult to remember, and there was no constant tendency in the direction of the colour memory shift. Accuracy was higher in the unmixed design, therefore it was concluded that the presence of other colour chips during the learning period (context) improves the accuracy of successive colour matching. However, it has to be noted that the unmixed design employed much more chips (672) than the mixed design (169), which could also have influenced the difficulty of the task. Some learning effects were also observed as observers proceeded with the experiments. The ability to remember monochromatic lights was tested for delays between 0.1 and 24.3 s in a delayed matching paradigm by Nilsson and Nelson (Nilsson & Nelson, 1981). The aim was to qualitatively measure how and to what extent the time delay influences the accuracy of short term colour memory performance and to further knowledge about storage process. 16 different monochromatic colours were employed as stimuli, with six different time delays ranging between 0.1 and 24.3 s. The reference stimulus was shown for 1 s and the observers were allowed to rehearse until they were satisfied with their answers. Following the time delay, observers were asked to set the remembered colour by adjusting wavelength. Minor shifts were found for some wavelengths (e.g. blue, red), in case of some interstimulus intervals, which were not consistent across colour categories. It was discovered that time delay causes a shift in memory but its further increase does not cause further variability or decrease in terms of accuracy. However, over longer delays

colours of short wavelengths were more likely to be matched with longer ones and wavelengths above 540 nm shifted more towards shorter ones. Their results showed that purple, green-blue, yellow and orange were remembered better which shows a similarity with the results of Jin and Shevell who found that colours of medium wavelengths are remembered better (Jin & Shevell, 1996). Based on the exponential pattern of a number of the hue shifts with time, it was assumed that for colour there exist different storage levels and mechanisms in short term memory. Monochromatic equiluminant stimuli using five different wavelengths as reference on a bipartite field in pairs with the test stimuli were presented in order to assess whether there were any differences in the ability to discriminate different wavelengths (possible hue shifts) at different time delays (Uchikawa & Ikeda, 1981). The decrease in performance and qualitative changes were measured as a function of time delay. The aim was to explore the memory deterioration within a short period of time (1 s) as well as to establish quantitative data of the time course of the wavelength discrimination deterioration during the first 6 s of visual short term memory. Relatively constant performance was found for up to 60 ms and then a gradual decline as the duration of the delay was increased until 190 ms beyond which the function did not further decrease. It was concluded that memory for the different hues deteriorates within a relatively short period of time. These findings are in accordance with the results of Nilsson and Nelson (Nilsson & Nelson, 1981) stating that simultaneous discrimination performance is about half as variable as successive. A wavelength matching experiment was carried out by Selinger (Selinger, 2002) in order to assess the wavelength dependence of colour memory with increasing time delays (1-30 s). Observers viewed the hue (monochromatic light) reproduced by a monochromator for 0.2-3 s, after which

another hue appeared on the other side of the bipartite field and the observer adjusted it in order to match the original colour. 14 reference hues were employed, the matched wavelengths were noted, and wavelength differences were calculated in terms of minimum detectable differences which were the highest and the most stable in the green region. The variability of the matches was different for the different colours but overall, discrimination thresholds were twice as high for memory matching than for simultaneous matching. The length of time the observer had to view the reference stimulus (exposure time) did not affect performance. The length of delays above 5 s (5 s, 10 s, 15 s) did not cause further deterioration in performance, but there was a significant difference between 1 s and 5 s delays. Non-monochromatic lights (non-spectral colours) that had low saturation were employed by D'Ath and colleagues (D'Ath et al., 2007) to further explore the results of Selinger and to examine whether they experience the same memory deterioration in case of this condition. Stimuli were 12 different coloured luminous surfaces (defined around a circle in CIE UCS 1976 chromaticity diagram) displayed on a monitor that observers viewed for 10 s, after which the hue was changed and the observer had to reset it to the remembered colour without delay and after one hour and one week, in terms of hue, while luminance and saturation remained constant. There was a significant difference for the memory performance in case of the different hues.

2.6.2.2 Memory Colours of Familiar Objects

There is evidence in the literature that memory colours of familiar objects tend to be remembered more accurately, possibly because people have a frequent visual experience with them, and it is likely that a long term representation of their typical colour is built up (Bartleson, 1960). The coloured patch that looked like a typical colour of a known object (green grass, evergreen tree, beach

sand) had to be chosen by the observers from selected Munsell test colours during the experiments of Bartleson (Bartleson, 1960). Even though the chosen objects had some inherent variability in terms of colour, saturation and brightness, there was a consistent minor shift in the remembered colours, most likely towards more impressive (salient) hues.

With the aim to investigate whether the physical attributes of colours or the interaction of various factors such as biological, social and linguistic influences have a greater impact on colour memory, a method was developed by Ratner & McCarthy (Ratner & McCarthy, 1990), where the stimuli were pictures of familiar objects with familiar focal colours (so-called ecologically relevant stimuli) within a contextual colourful surround. Memory for focal colours, as well as memory for typical colours of familiar objects, were examined using four different conditions; focal-appropriate, focal-inappropriate, nonfocal-appropriate and nonfocal-inappropriate. In the 'appropriate' case, the stimulus had a meaning, which enabled the parallel investigation of influences of the different factors, i.e. appropriateness of colours was varied to investigate if it had the same effect as the focality of colours. Observers were asked to choose the memorized colours out of three samples, the colours of which were adjacent on the Munsell chart or had slightly different brightness. The original premise was that appropriateness of a certain colour was more of a determining factor than were focal colours. It was found, that colours of typical objects were remembered more accurately when coloured pictures of familiar objects with typical colours (instead of non-typical colours) were presented to observers in a memory task. The results confirmed that colours of familiar objects were significantly better retained than focal colours, which implies that cultural issues have a remarkable impact on colour memory and focal colours did play a lesser role than it had been

assumed previously. The possible deviating effect of shape and texture on colour perception and memory was investigated by Siple and Springer (Siple & Springer, 1983), as well as whether reproducing colours with a computer had any impact on performance. It was also investigated whether there were any preferred colours in colour memory. According to the results, hue was quite accurately remembered. As opposed to Bartleson (Bartleson, 1960) and Newhall et al (Newhall et al., 1957), their subjects tended to choose lower Munsell values, but greater chroma in memory than the test ones. It was also assumed that colour, shape and texture information were processed in different pathways, since changes in shape and texture did not influence the accuracy of colour memory. Colour seemed to be an independent property in memory and perception. However, colours in context were chosen quicker, so it may possibly be an attribute that enhances colour memory.

2.6.2.3 Memory Colour and Context

The process of memorizing colours of complex scenes is still not thoroughly understood. Loftus (Loftus, 1977) performed an experiment, where subjects observed coloured scenes. After that, one group was asked to name the colour of a certain object, the other were not before they had been given misleading information about a colour of that certain object on the scene. Over time, memory colours shifted systematically towards the incorrect hue that was given to them, but the group who named the remembered colour tended to be more accurate and the hue shifted less. Francis & Irwin (Francis & Irwin, 1998) investigated whether the surrounding of a colour contributes to memory, which would result in changes in the pattern of the decay or the accuracy in memory. Separate colour patches or colours were presented on either a Clip-art, or a Mondrian image, and it was found that the presentation of a context improved

memory, independent of the kind of coloured stimuli that had been shown. Coloured patches that were presented on their own, were remembered the worst. Amano and colleagues (Amano et al., 2002) studied memory for colours of natural scenes. According to their findings, subjects tended to detect reduction in luminance and chromatic contrast easier as opposed to an increase, which implies that colours are remembered as being more salient than they actually are. They also noted that within category changes in colour were more difficult to notice as opposed to cross-category changes.

2.6.2.4 Categorization and Colour Memory

Heider (Heider, 1972) based her experiments on the hypothesis, that focal colours that are linguistically coded can be remembered more easily and also emphasised the role of colour saliency (Brown & Lenneberg, 1954; Burnham & Clark, 1955; Krauss, 1968). During perception and memory tasks, we tend to verbally code focal colours. Based on the hypothesis that language coding of colours can allocate memory coding, Heider (Heider, 1972) used observers of different nationalities and they found that the ability of naming colours did not significantly improve the accuracy of colour memory. However, focal colours that had the shortest names were recognized the most accurately. Later on, Lucy & Shweder (Lucy & Shweder, 1979) reproduced Heider's experiment but they failed to introduce a new method to find how colour memory is influenced by cultural factors. Garro (Garro, 1986) repeated their experiments one more time and eventually came to the conclusion that focal colours are indeed remembered better than non-focal colours. The only difference between the two experiments was that Garro insisted on keeping complete silence during the 30 s time delay interval whereas Lucy & Shweder allowed conversation. Based on this difference, during a repeated set of experiments without allowing

conversation, Lucy & Shweder (Lucy & Shweder, 1988) ultimately concluded the same results as Garro.

2.6.2.5 Saturation and Colour Memory

Saturation refers to the 'colourfulness' of a stimuli at a given brightness level. Irrespectively of the employed methods, stimuli or time delay, the most consistent and prominent shift in colour memory occurs in the dimension of saturation (Bartleson, 1960; Hamwi & Landis, 1955; Newhall et al., 1957; Siple & Springer, 1983; Uchikawa, 1983). Most of the experiments examined saturation shifts, as well as hue and brightness changes, whereas Uchikawa examined memory for saturation only (Uchikawa, 1983). There is a general agreement, that saturation increases in memory - which might also be part of the fact that there is a shift towards more salient colours - (Bartleson, 1960; Hamwi & Landis, 1955; Ling & Hurlbert, 2008; Newhall et al., 1957; Siple & Springer, 1983; Uchikawa, 1983) besides a few examples, where the changes were found inconsistent (Jin & Shevell, 1996; Perez-Carpinell et al., 1998). Hamwi & Landis (Hamwi & Landis, 1955) found that the chosen colours were more saturated in memory and opposite to what they expected, this tendency was less significant in case of their second experiment, and results were more variable in case of the unmixed design as explained in detail in **section 2.6.2.1**. In the experiment of Ling and Hurlbert (Ling & Hurlbert, 2008) the stimuli were coloured patches lit by different illuminants in a 3D setup, and for each reference stimuli they had a selection of test patches that varied in terms of hue or in terms of saturation only. They found an increase in saturation in memory under various illuminants. There is also a significant shift towards more saturated colours in case of typical colours of known objects (Bartleson, 1960; Newhall et al., 1957; Siple & Springer, 1983). In a supplementary experiment

examining the colours of eight known objects from Munsell chips, Newhall found that there was an increase in saturation when colours had to be recalled from memory. In the experiment of Bartleson (Bartleson, 1960) the memory colours of ten familiar objects were studied, the observers had to choose the one from the Munsell test patches which looked like a typical colour of a known object (green grass, evergreen tree, beach sand). Even though the objects had some variability, the results showed increased saturation. According to the results of Siple & Springer (Siple & Springer, 1983), in case of familiar objects there was a shift in saturation towards highly saturated colours. To study colour memory for non-spectral colours, Uchikawa (Uchikawa, 1983) chose seven wavelengths and varied their purity by adding white light to them in different proportions. They used the term ‘purity’ for defining the amount of white light the stimulus contained, referring to saturation. To determine purity discrimination thresholds first, observers were presented with the stimuli simultaneously, and they had to decide if the test colour was less or more saturated than the reference one. The same experiments were repeated with a 3 s delay and purity discrimination for delayed matching was measured as well. Both test and comparison stimuli were coloured and purity varied between 0.0-1.0, depending on the amount of white light added and were expressed by their position on the CIE1931 xy chromaticity diagram. According to the results, discrimination ability was more accurate in simultaneous, than in successive matching tasks. In the memory task, the discrimination threshold was significantly larger, with a proportion of about two, when compared to the simultaneous matching, therefore, in accordance with earlier publications, saturation shifts in successive matching were found, towards increased saturation (Hamwi & Landis, 1955; Newhall et al., 1957; Nilsson & Nelson, 1981). They showed that there was a decrease in

accuracy when observers made judgements about purity over time delay. Perez Carpinell et al. (Perez-Carpinell et al., 1998) examined memory for eight familiar object colours on 100 observers, who had to choose the remembered colours out of 80 different NCS (Natural Color System) colour samples and found that the saturation increased in cases where the original colour had high saturation, and decreased or remained unchanged when the original colour had low saturation and these changes also depended on the type of illumination they used.

2.6.2.6 Brightness and Colour Memory

Brightness is an important property of colours, it is a perceptual phenomenon that correlates to the physical intensity of the light that is emitted from a source (monitor) or reflected by a surface. The results in this area are quite diverse, some groups found an increase in brightness (Bartleson, 1960; Newhall et al., 1957), some a decrease (Hamwi & Landis, 1955), a few concluded it was very accurate (Siple & Springer, 1983) and some found that it depended on the original brightness; dark ones remembered as darker, light ones remembered as even lighter. Hamwi and Landis (Hamwi & Landis, 1955) discovered that observers tended to choose darker colours and that a colourful background improved performance. According to Newhall et al. (Newhall et al., 1957), the memory matched colours required higher luminance values for the match compared to the simultaneously matched ones. Bartleson (Bartleson, 1960) showed that there was an increase in brightness for the memory of colours of natural objects. Siple & Springer (Siple & Springer, 1983) claims that in case of object colours, the brightness change is minimal, therefore it is different from the findings of others (Bartleson, 1960; Newhall et al., 1957), namely, that light colours become lighter and dark colours become darker. In order to examine

how accurately brightness differences are retained in memory, Uchikawa & Ikeda (Uchikawa & Ikeda, 1986) studied the accuracy of successive versus simultaneous matching for colours of different brightness in the range between 410 nm and 670 nm. Each of the seven colours that were used as references were compared with stimuli of the same hue but of ten different luminance levels and the task was to compare the brightness levels (heterochromatic brightness matching). They also examined the specific influence of individual wavelengths on the brightness shifts. Stimuli were presented in a circular bipartite field. They found deterioration in the accuracy of brightness discrimination over the 6 and 11 s time delays they had employed. In case of most colours there was a shift towards darker ones and when compared to simultaneous matching, the performance during the memory task was 50% less accurate. In a second experiment, they employed a mask stimulus of two different luminance levels, but of same hue as the reference. Its onset was at 6 s during the 11 s time delay and they found that it further disrupts the memory performance for the luminance of coloured stimuli. In the case when the mask was brighter, the shift occurred in the brighter direction, and when it was darker, there was a shift in the darker direction. In the experiment of Sachtler & Zaidi (Sachtler & Zaidi, 1992) higher brightness intensities were needed to discriminate between colours. There was an agreement that there is a greater visual capacity to remember colour than brightness cues.

2.6.3 Memory for Spatial Frequency

In this thesis we also examined VSTM for spatial frequency and velocity, therefore in this section I briefly review previous literature in this area.

VSTM for spatial frequency is highly accurate according to psychophysical studies. Magnussen and co-workers employed a delayed discrimination paradigm to examine VSTM for the spatial frequency of sinusoidal gratings (**Figure 2.12**) (Magnussen et al., 1990). They used 1-30 s delays, and found that delayed discrimination ability for spatial frequency remained highly accurate with increasing time delays (Magnussen et al., 1990).

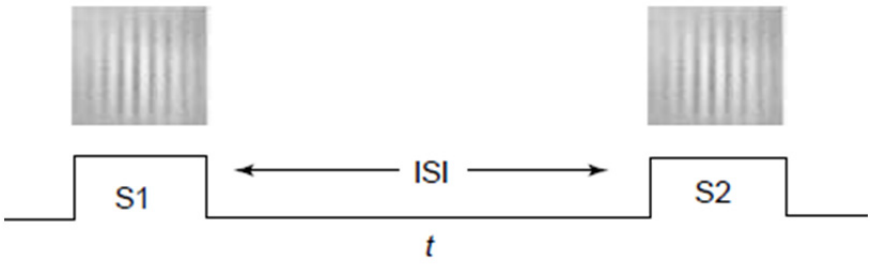


Figure 2.12 Illustration of a typical delayed discrimination paradigm. Reference and test sinusoidal gratings are presented with variable time delays (ISI), and the observer is asked to decide whether the two gratings are the same or different for the examined stimulus dimension (e.g. spatial frequency, contrast, orientation, speed and direction of motion) or, which of the two gratings has a higher value in terms of the examined stimulus dimension (Source: (Magnussen, 2000)).

When they examined how other stimulus attributes affect this accuracy, they found that relative orientation of the grating caused no interference (Magnussen et al., 1990) and spatial frequency of the grating slightly increased thresholds for simultaneous discrimination, which did not further increase during the memory task (Magnussen et al., 1990; Magnussen et al., 1996). Contrast had the greatest influence on discrimination ability, but as in case of spatial frequency, it did not cause further decrease with time delay (Magnussen et al., 1990; Magnussen et al., 1996).

Brain imaging studies of delayed spatial frequency matching showed activation of striate, extrastriate, parietal and prefrontal areas during the control, as well as the memory tasks, but activity was generally higher during the memory tasks (Greenlee et al., 2000), and there were no hemisphere differences except for

the insular cortex, where activity was found in the right hemisphere only. They also hypothesized based on the results, that the parietal cortex is responsible for the delayed discrimination of basic stimulus dimensions. The task was to compare spatial frequencies in memory in a two-alternative forced choice procedure, as compared to a simple detection of the grating, which served as control. The reference stimulus had a spatial frequency of 2 c/deg.

Retention of information about the orientation of gratings is also highly accurate in memory (Magnussen et al., 1985). Some studies have demonstrated a decrease in performance with ISI (Magnussen et al., 1996; Magnussen et al., 1998). This ability is not decreased by changes in the spatial frequencies of the gratings (Magnussen et al., 1998).

Baumann et al. carried out an experiment, where they examined the brain regions that activated when observers carried out spatial frequency discrimination tasks (8 s delay, spatial frequency = 3-9 c/deg) on gratings of different orientations, in order to explore the effect of a task irrelevant stimulus dimension on the activation pattern (Baumann et al., 2008). They found stronger bilateral activity in V1, V2, when the gratings were orthogonal, compared to similar orientations, implying that a non-relevant stimulus attribute places an extra demand on visual areas. Overall, there was no significant increase in activity as a result of the grating orientation in the dorsolateral part of the prefrontal cortex (DLPFC) and in the parietal cortex, suggesting that it exploited only low level mechanisms. Although discrimination thresholds were not elevated, the change of the orientation in the spatial frequency discrimination task resulted in increased reaction times, which could imply their processing was not completely separated.

Magnussen (Magnussen et al., 1996) employed a delayed discrimination task to examine VSTM for contrast of sinusoidal gratings. They used 1-10 s delays and found a significant decrease in discrimination ability with increasing time delay (Magnussen et al., 1991). The contrast and spatial frequency of the reference stimulus did not interfere with memory performance.

2.6.4 Velocity and Motion

The middle temporal area (MT/V5), also known as the centre for visual motion, has been extensively studied in macaques (Bisley et al., 2001; Zaksas & Pasternak, 2006). In a psychophysical study on macaques, the test and the reference stimuli were presented with a 1500 ms delay in a two-interval forced choice procedure (Pasternak & Zaksas, 2003). The macaques had to decide whether the directions of the moving dots in the test stimulus were the same or different than the reference. The results showed that introducing a time delay did not decrease the accuracy of the discrimination ability. When they introduced a masking stimulus, they found that its size and location interfered with the accuracy only in some specific cases, namely, when it appeared at the same location and its size matched the remembered sample.

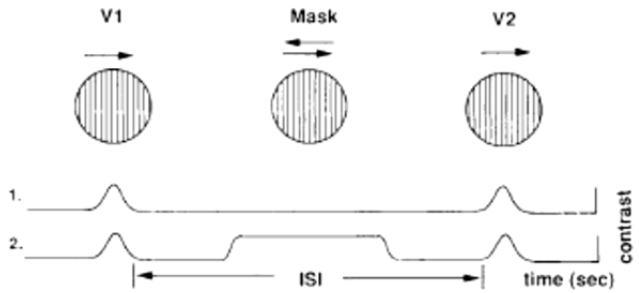


Figure 2.13 A schematic representation of the two-interval forced choice procedure for delayed velocity discrimination. The observer is asked to, after variable time delays, decide, which of the drifting stimuli, V1 and V2 has the higher velocity. In one set of experiments, the ISI is filled with a blank screen, and in a second set of experiments a masker grating is exposed during the ISI (Source: (Magnussen & Greenlee, 1992)).

Magnussen and Greenlee (Magnussen & Greenlee, 1992) determined velocity discrimination thresholds for drifting luminance gratings using the delayed matching paradigm (**Figure 2.13**), and found that the accuracy for velocity remained very high in VSTM with increasing time delays. Masks only interfered with memory processes when they had a significantly different velocity to the reference stimulus. When two different stimulus attributes were combined, memory masking was only effective within the same dimension and accuracy was dependent on the spatial and temporal frequency of the grating.

Recent studies investigated whether this area has a role in the storage of motion information as well (Bisley et al., 2004; Bisley et al., 2001; Magnussen & Greenlee, 1992; Pasternak & Zaksas, 2003; Zaksas & Pasternak, 2006). Intracellular recordings (Bisley et al., 2004) showed activity of neurons in MT during a match-to-sample task, where monkeys compared the direction of moving dots in a two-interval forced choice test. The activity of MT neurons remained higher than baseline during the delay. PFC showed delay related activity as well during the task (Zaksas & Pasternak, 2006). Moreover, clinical studies on patients with brain damage in the posterior temporal cortex found that this area is responsible for the short term storage of velocity (Greenlee et al., 1995).

In this work we aimed to investigate the organisation of visual information in VSTM with psychophysical methods, with special interest in colour, spatial frequency and velocity. Previous studies of VSTM have indicated the existence of specific memory mechanisms for visual attributes such as orientation, spatial frequency, velocity, contrast and colour and we aimed to further explore these issues in view of the present knowledge about sensory processing and the storage of visual information.

Chapter 3

General Methods

3.1 Introduction

In this chapter I describe the stimulus display equipment, calibration procedures, stimulus structure, experimental paradigms, data analysis methods and observer inclusion criteria that were employed during the experiments described in subsequent chapters.

3.2 Colour Stimuli

3.2.1 Stimulus Presentation

All colour stimuli were displayed on a high resolution 21" Sony FD Trinitron CRT (cathode ray tube) monitor (GDM500; Sony, Tokyo, Japan), with a refresh rate of 120 Hz. The stimuli consisted of single or pairs of coloured circular hard edged patches and their diameter subtended 1.5° - 3° of visual angle (**see Figure 3.1**). Stimuli were defined in CIE xy (1931) colour space based on the 2° standard observer (i.e. stimuli were viewed through an aperture of 2°) (**Table 3.1 and Figure 3.2**) and were expressed as vectors in MBDKL colour space (after MacLeod, Boynton, Derrington, Krauskopf and Lennie) (Derrington et al.,

1984; Krauskopf et al., 1982; MacLeod & Boynton, 1979). The stimuli were presented on an equiluminant grey background, with a luminance equal to 12.5 cd/m^2 (illuminant C, CIE co-ordinates: x=0.310, y=0.316). Stimuli were generated using NewRT 1991, a custom in-house built software that drove a VSG 2/5 video graphics card (Visual Stimulus Generator; Cambridge Research Systems Ltd., Rochester, UK).

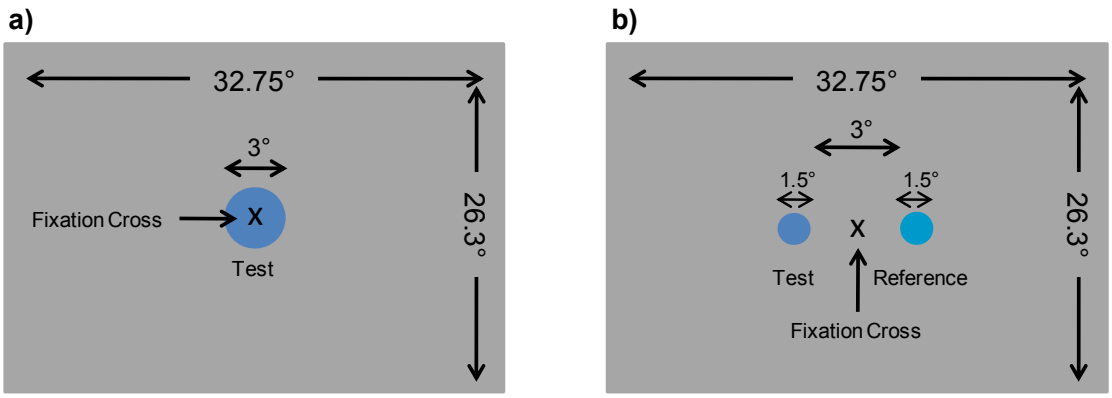


Figure 3.1 Stimulus presentation and configuration for the a) hue scaling experiment and, b) colour memory experiment (presented in **Chapter 4**). In case of the colour memory masking experiment, an additional, masking stimulus was presented at the position of the fixation cross which subtended 1.5° (presented in **Chapter 5**).

3.2.2 Colour Specification

In this section the colour spaces relevant to the present study are discussed, namely, the CIE 1931 XYZ colour space, CIE L*a*b* colour space as well as the MBDKL colour space in which the stimuli were defined in our experiments. These colour systems were chosen to describe the chromatic properties of the employed stimuli, due to the fact that they have traditionally been used in a wide variety of colour vision experiments and are universally accepted in colour research (De Valois et al., 1997b; Derrington et al., 1984; Krauskopf et al., 1982).

3.2.2.1 CIE1931 xy Colour Space

All the coloured stimuli used in these experiments were defined according to their coordinates in CIE 1931 xy colour space. The CIE1931 xy colour space (**Figure 3.2**) is a standardized system for colorimetry and was introduced by the Commission Internationale de l'Eclairage (CIE, International Commission on Illumination) with the aim to work out a colour representation system for practical colour measurements and specification (Guild, 1931; Wright, 1928). It is based on colour matching functions of the standard observer (normal population) for the 2° viewing conditions (i.e. the stimuli were shown in an aperture that subtended 2° of visual angle), which are given as r(λ), g(λ) and b(λ) (**Figure 3.3**) (Guild, 1931; Wright, 1928). These functions were defined in colour matching experiments, where the observers were asked to change the relative content of one hemifield for three primaries (wavelengths: 435.8 nm, 546.1 nm, 700 nm) to match the monochromatic light presented in the other side of the field.

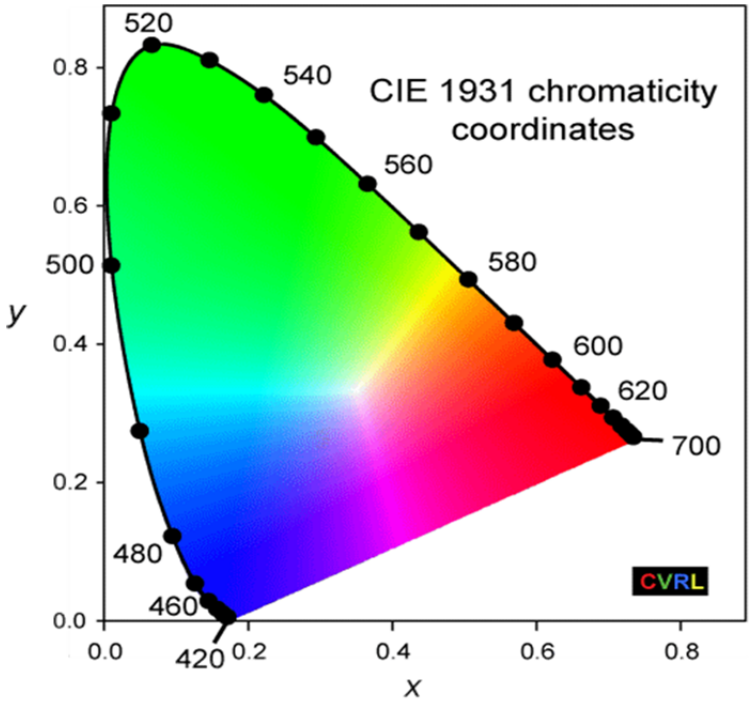


Figure 3.2 CIE1931 xy colour space showing the spectrum locus (continuous line) and spectral wavelengths at every 10 nm (filled circles). A representation of the colour of each coordinate is

shown. CIE (1931) xy chromaticity space is based on colour matching functions of the standard observer (normal population) for 2° viewing conditions (Stockman, A. (2004). “Colorimetry”. In T. G. Brown, K. Creath, H. Kogelnik, M. A. Kriss, J. Schmit & M. J. Weber (Eds.), “The Optics Encyclopedia: Basic Foundations and Practical Applications (Vol. 1, pp. 207-226)”. Berlin: Wiley-VCH. Available at: <http://www.cvrl.org/> [Accessed 24 August 2010])

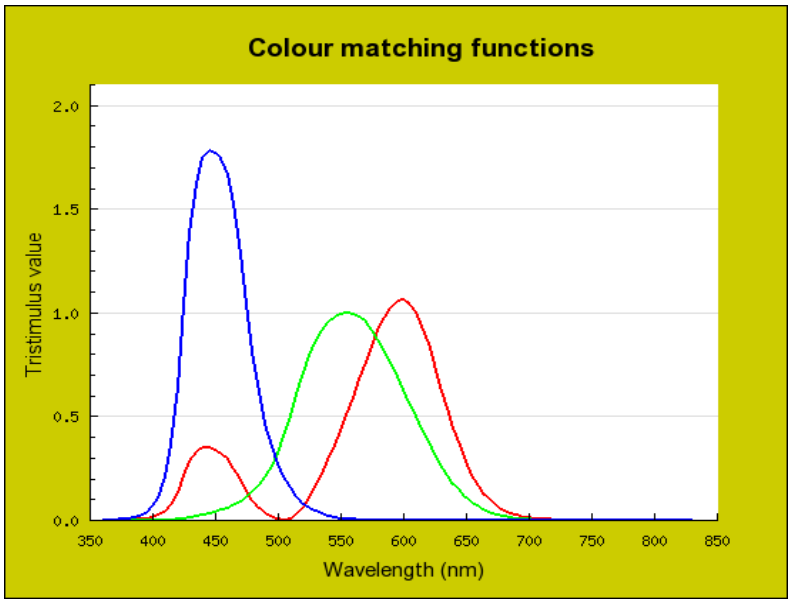


Figure 3.3 CIE (1931) x(λ), y(λ) and z(λ) tristimulus functions. The tristimulus functions were calculated from the colour matching functions, which are based on the additive mixing of the three preset monochromatic primaries (Guild, 1931; Wright, 1928) ((n.d) [Online Image at http://www-cvrl.ucsd.edu/cmfs.htm] Available at: <http://courses.washington.edu/css451/2010.Winter/FinalProjects/Results/5.Spectrum/SpectralProject.pdf> [Accessed 23 August 2010]).

In order to overcome the problem that some colour matching functions give negative amounts, the r(λ), g(λ) and b(λ) colour matching functions were converted into x(λ), y(λ) and z(λ) tristimulus functions under the assumption that all x(λ), y(λ) and z(λ) tristimulus functions should be positive values. XYZ tristimulus values were calculated by taking both the spectral power distribution and the colour matching functions of the human observer into account (Kaiser & Boynton, 1996). Y(λ) was defined as the photopic luminous efficiency function (V_λ) by CIE, therefore the Y tristimulus value can be easily measured to establish the luminance (L) of a given colour.

$$X = K_m \int L_{e,\lambda} x(\lambda) d\lambda \quad (3.1)$$

$$Y = K_m \int L_{e,\lambda} y(\lambda) d\lambda \quad (3.2)$$

$$Z = K_m \int L_{e,\lambda} z(\lambda) d\lambda \quad (3.3)$$

Where, K_m is the maximum photopic luminous efficacy (l_m/W). The values, *x*, *y* and *L* are the chromaticity coordinates of the CIE1931 xy colour space and are calculated the following way from the tristimulus values:

$$x = \frac{X}{(X+Y+Z)} \quad (3.4)$$

$$y = \frac{Y}{(X+Y+Z)} \quad (3.5)$$

$$L = Y \quad (3.6)$$

All visible colours are represented on the chromaticity diagram, the white point is located in the centre and saturation gradually increases towards the loci of spectral colours. **Figure 3.2** illustrates an equiluminant plane of CIE 1931 xy colour space. The main disadvantage of this colour representation system is that it is not perceptually uniform, equal distances on this diagram do not represent equal differences in terms of colour appearance. MacAdam (MacAdam, 1942) examined colour discrimination for a wide range of colours on the CIE 1931 xy chromaticity diagram and defined ellipses around each of these locations within which the colours are not discriminable from one another (**Figure 3.4**) (MacAdam, 1942). He found that these ellipses are of different size depending on their location in the CIE 1931 xy chromaticity diagram. To address the problem of perceptual non-uniformity, namely, that equal distances in CIE1931 xy chromaticity diagram do not represent perceptually equal differences (MacAdam, 1942), the more perceptually equal CIE'Lab and CIE'Luv' colour spaces were developed (**Section 3.2.2.3**).

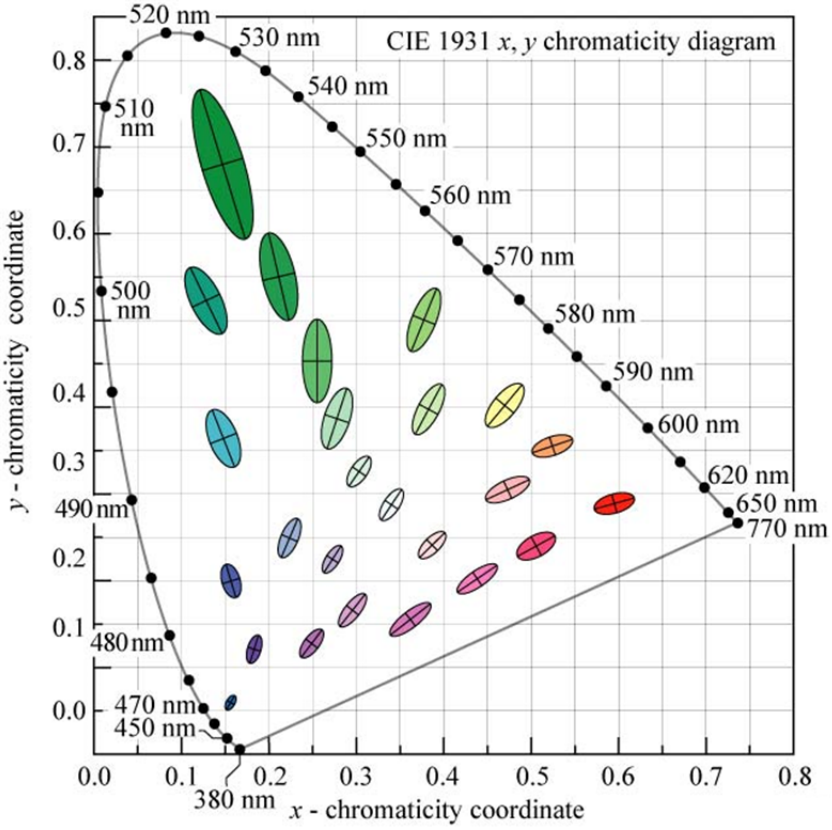


Figure 3.4 MacAdam ellipses, plotted on the CIE 1931 xy chromaticity diagram (Schubert E.F. (n.d.) [Online Image] Available at: <http://www.ecse.rpi.edu/~schubert/Light-Emitting-Diodes-dot-org/chap17/F17-05%20MacAdam%20ellipses.jpg> [Accessed 23 August 2010]) (MacAdam, 1942; Wright, 1928).

3.2.2.2 MBDKL Colour Space

The MBDKL colour space (**Figure 3.5**) was developed from the MacLeod and Boynton cone excitation diagram, and incorporates a luminance dimension as well (Derrington & Lennie, 1984; Desimone et al., 1984; Krauskopf et al., 1982; MacLeod & Boynton, 1979). This colour space is based on linear combination of cone signals and therefore represents stimuli that excite the three cardinal post-receptoral channels (L/M, S/(L+M) and L+M) (Krauskopf et al., 1982), corresponding to colour encoding at a relatively early stage of the visual system (Derrington et al., 1984). The L/M cardinal direction corresponds to the 0° - 180° axis, it activates L and M cones and affects S cones to a minor extent. S/(L+M) cardinal axis corresponds to the 90° - 270° axis in MBDKL colour space, which stimulates S cones and keeps M and L cone activation at a constant level. The

two chromatic axes define an isoluminant plane and the luminance channel is positioned perpendicular to this, establishing the third direction in the colour space. The intersection of the three axes defines the white point. Variations in hue i.e. chromatic axes along the isoluminant plane are expressed as vectors, specified by ϕ (azimuth). Changes in the angle Θ away from the isoluminant plane produces stimuli with increasing amount of luminance contrast content. The length of the vectors (i.e. their distance from the centre) defines the saturation or purity of the chromatic stimulus.

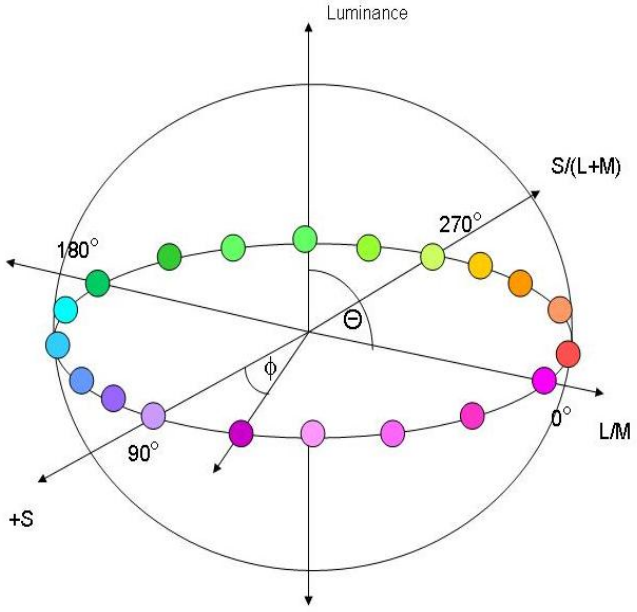


Figure 3.5 Illustration of the MBDKL colour space and the representative locations and modulations of the 20 stimuli on an isoluminant plane, which were employed during the hue scaling experiments. ϕ represents chromaticity and Θ denotes changes in luminance. The capital letters indicate the weighted inputs of the cones into the cone opponent mechanisms. S cone input varies along the 90° - 270° axis whereas L and M cone excitations vary along the 0° - 180° axis. In case of the intermediary colours that are depicted here there is a combination of the activation of these mechanisms (Modified after: (Krauskopf et al., 1982)).

This system is widely employed by scientific groups which examine post-receptoral colour processing because hues are easy to compute and selective activation of colour opponent channels is feasible. Isoluminant stimuli including spectral and non-spectral hues can also be defined in this colour space. The advantage of MBDKL colour space is that colours can be generated that lie

along the cardinal axes and hence stimulate the physiologically important cone opponent mechanisms which are operational in the sub-cortical visual pathway At the same time, other stimuli which represent more, perceptually based colour categories (e.g. red, green and blue) can also be generated using this colour space. Such stimuli have a special importance because they represent colours that are processed at higher cortical levels (Conway, 2003; De Valois & De Valois, 1993; Xiao et al., 2007). As with the CIE xy 1931 chromaticity diagram, the disadvantage of MBDKL space is that it is not perceptually uniform, therefore equal distances on this diagram do not represent equal differences in colour appearance.

The chromatic stimuli presented in the experiments were defined by CIE xy 1931 chromaticity coordinates, and expressed as vectors in MBDKL colour space. The chromaticities (saturation) of the stimuli were given as equal length vectors in MBDKL colour space that originated from illuminant C and formed a circle on the isoluminant plane equally spaced around the white point in steps of $\phi = 18°$ ranging from $\phi = 0°$ to $\phi = 360°$ on an isoluminant plane (Y = 12.5 cd/m^2) (**Figure 3.5**). The CIE 1931 xy stimulus coordinates, which were employed in the initial experiments are represented in **Table 3.1**. The background was uniform grey of luminance equal to 12.5 cd/m^2, defined as the white point (CIE 1931 chromaticity coordinates; x = 0.310, y = 0.316, illuminant C).

Table 3.1 CIE1931 xy chromaticity coordinates of stimuli employed in the initial hue scaling experiments and their ϕ angle in MBDKL colour space. In all cases Y = 12.5 cd/m^2.

Chromatic Axis (ϕ)	x coordinates	y coordinates
0°	0.373	0.268
18°	0.360	0.251
36°	0.333	0.240
54°	0.309	0.237
72°	0.284	0.241
90°	0.262	0.253
108°	0.245	0.270
126°	0.234	0.293
144°	0.231	0.317
162°	0.235	0.342
180°	0.247	0.364
198°	0.264	0.381
216°	0.287	0.392
234°	0.311	0.395
252°	0.336	0.391
270°	0.358	0.379
288°	0.375	0.362
306°	0.386	0.339
324°	0.389	0.315
342°	0.385	0.290
Background	0.310	0.316

3.2.2.3 CIE 1976 L*a*b* Colour Space (CIELAB)

As mentioned above, equal distances in the CIE 1931 xy chromaticity diagram do not represent perceptually equal differences between two colours (MacAdam, 1942). The MacAdam ellipses represent areas within which the typical observer is unable to discriminate between two colours and it is apparent from **Figure 3.4** that these ellipses have a substantially different size depending on their location in the colour space. In order to unify the description of colour stimuli used, the CIE 1976 L*a*b* space was developed as a nonlinear transformation from CIE 1931 XYZ space in 1976. In CIE 1976 L*a*b* space L* represents luminance and a* and b* represent the chromatic components

(**Figure 3.6**). In this colour space equal Euclidean distances represent equal perceptual differences between colours.

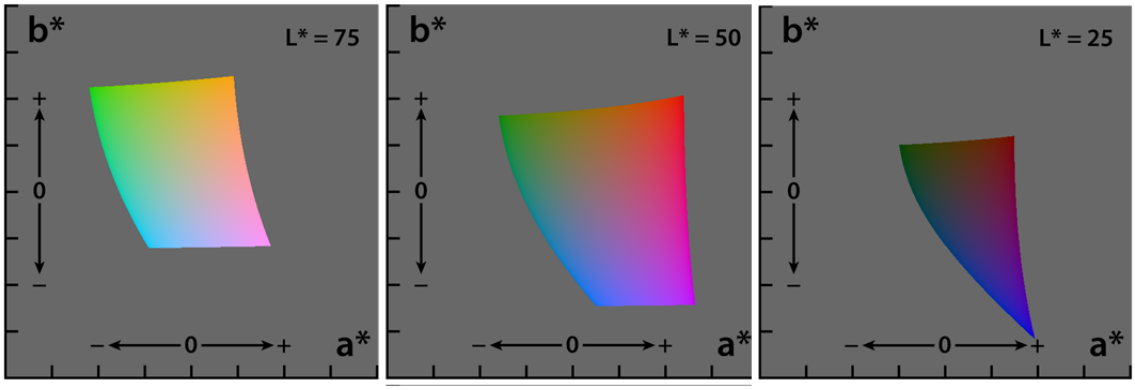


Figure 3.6 Illustration of CIE 1976 L*a*b* colour space (CIELAB) at different luminance levels. (Wikipedia (n.d.) [Online Image] Available at: <http://en.wikipedia.org/wiki/Lab_color_space> [Accessed 25 August 2010]).

3.2.2.4 CIE Calculations

Initially, hue shift values in the colour memory experiments were expressed as vector rotations in MBDKL space and afterwards, to further address the problems that arise from the perceptual non-uniformity of MBDKL colour space and CIE1931 xy standard chromaticity diagram, the hue shift values in terms of CIE1931 xy chromaticity coordinates were first calculated and then converted into distances in the more perceptually uniform CIE L*a*b* space. The conversion from the CIE1931 xy to CIE L*a*b* space was carried out the following way (Wyszecki & Styles, 2000):

$$x = \frac{X}{(X + Y + Z)} \tag{3.7}$$

$$y = \frac{Y}{(X + Y + Z)} \tag{3.8}$$

$$z = \frac{Z}{(X + Y + Z)} \tag{3.9}$$

$$z = 1 - x - y \tag{3.10}$$

$$X = \frac{x}{y} \cdot L_v \tag{3.11}$$

$$Y = L_v \tag{3.12}$$

$$Z = \frac{z}{y} \cdot L_v = \left(\frac{1 - x - y}{y} \right) \cdot L_v \tag{3.13}$$

Where, *X*, *Y* and *Z* represent the tristimulus values of the test colour, *x*, *y* and *z* represent the CIE 1931 chromaticity coordinates. In the following step, CIEL*a*b* coordinates were calculated from the XYZ tristimulus values the following way:

$$L* = 116 \cdot \left(\frac{Y}{Y_n} \right)^{\frac{1}{3}} - 16 \tag{3.14}$$

$$a* = 500 \cdot \left[\left(\frac{X}{X_n} \right)^{\frac{1}{3}} - \left(\frac{Y}{Y_n} \right)^{\frac{1}{3}} \right] \tag{3.15}$$

$$b* = 200 \cdot \left[\left(\frac{Y}{Y_n} \right)^{\frac{1}{3}} - \left(\frac{Z}{Z_n} \right)^{\frac{1}{3}} \right] \tag{3.16}$$

Where X_n, Y_n and Z_n represent the tristimulus values of the specified white point (in the present case; X_n=12.263, Y_n=12.5, Z_n=14.794) (Wyszecki & Styles, 2000).

This transformation was used in the experiments described in **Chapter 4**.

3.2.3 Phosphor Characteristics and Monitor Calibration

3.2.3.1 CRT Phosphor Coordinates and Spectral Characteristics

For a given CRT monitor the colour co-ordinates of its three phosphors can be measured and when converted to CIE 1931 xy values they define a triangular

region in CIE xy colour space (**Figure 3.7**). This represents the gamut of the monitor, the range of colours a monitor is able to display. The monitor phosphors of our experimental display are located on the corners of this triangle at the following coordinates: red (x = 0.5949, y = 0.3431), green (x = 0.2876, y = 0.5913) and blue (x = 0.1582, y = 0.0792), measured at a luminance of Y=12.5 cd/m^2 (x = 0.310, y = 0.316).

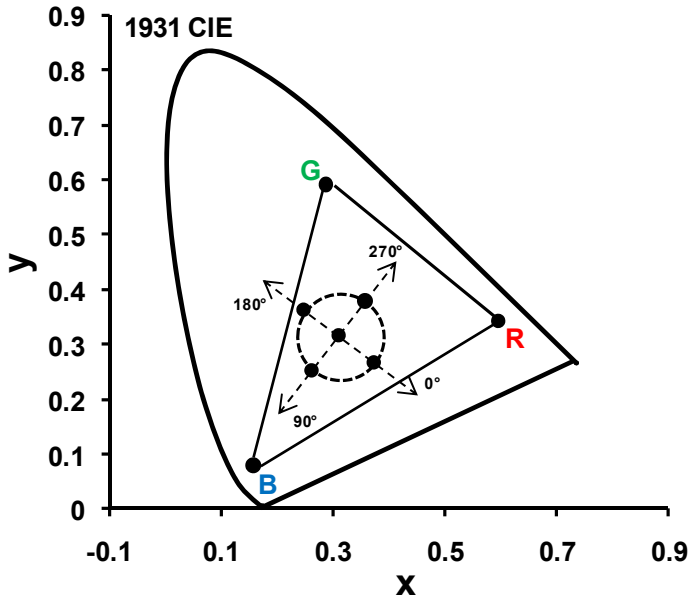


Figure 3.7 Gamut of the monitor defined by the three phosphors, Blue, Green and Red. Hues of equal saturation on the isoluminant plane are indicated by the circle, and cardinal axes in MBDKL colour space are indicated by axes 0° - 180° and 90° - 270°.

The spectral power distributions of the light emitted by the three phosphors of the monitor are shown on **Figure 3.8**. The measurements were taken using a PR650 Spectrascan SpectraColorimeter (Photo Research Inc., USA) and the graphs plot radiance as a function of wavelength for the blue, green and red phosphors (RGB values; red: 255,0,0; green: 0,255,0; blue: 0,0,255).

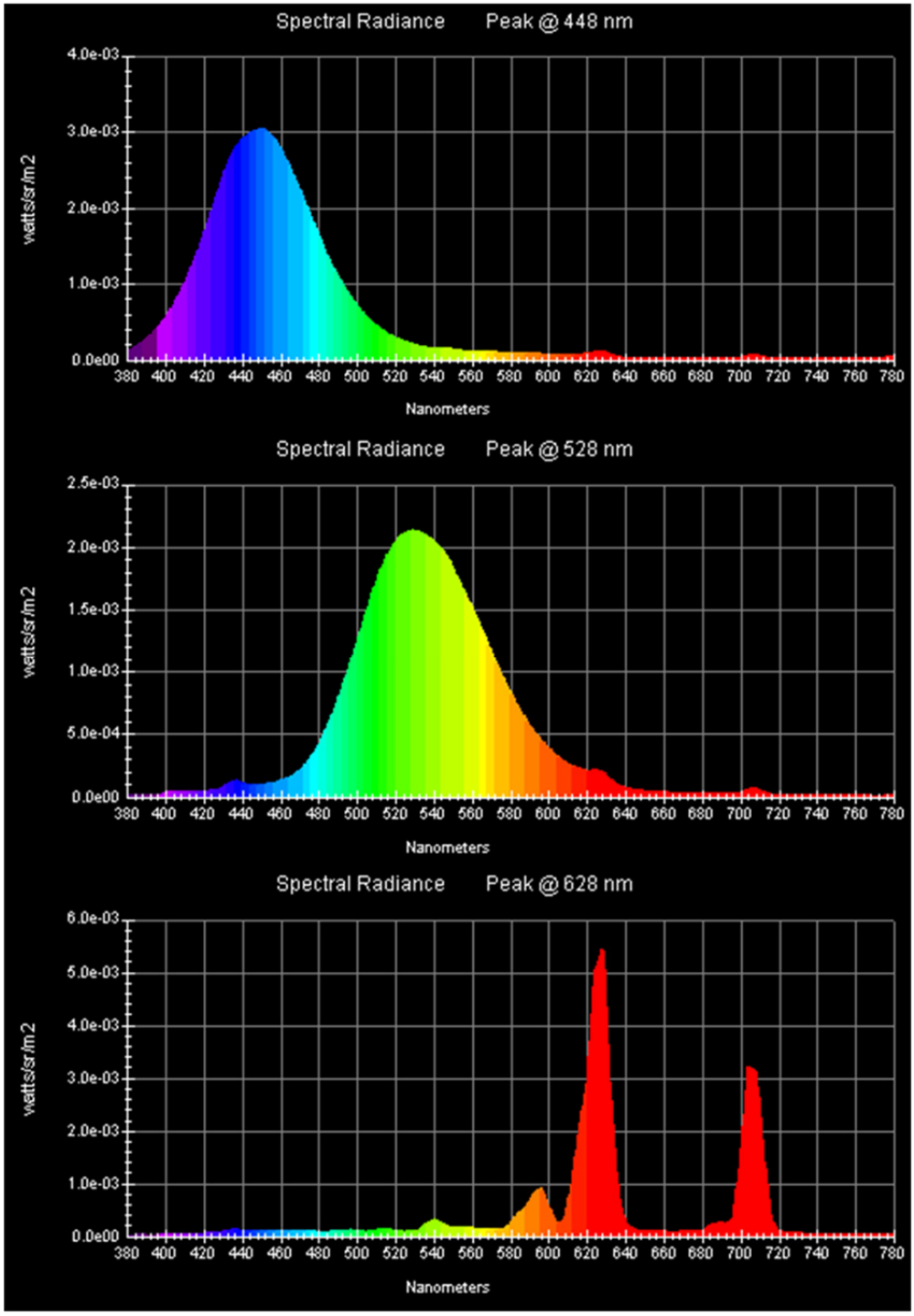


Figure 3.8 Phosphor spectral radiance curves of the individual blue, green and red phosphors of the Sony GDM 500 CRT monitor (Tokyo, Japan). Measurements were taken with a PR650 SpectraColorimeter (Photo Research Inc., USA). The graphs represent the spectral wavelength compositions of the light emitted by the monitor phosphors.

3.2.3.2 CIE Colour Calibration

Calibration of the stimulus display equipment is essential in order to control and describe the spatial, temporal, chromatic characteristics of the stimuli. Calibration was performed regularly during the course of these experiments.

CIE colour calibration was carried out using a PR650 Spectrascan SpectraColorimeter. The output of the monitor was measured for 20 different vectors in MBDKL space (**Table 3.1**) and the input values were modified accordingly in order to yield the desired output values. The input- and measured output values for the stimuli are shown on **Figure 3.9**.

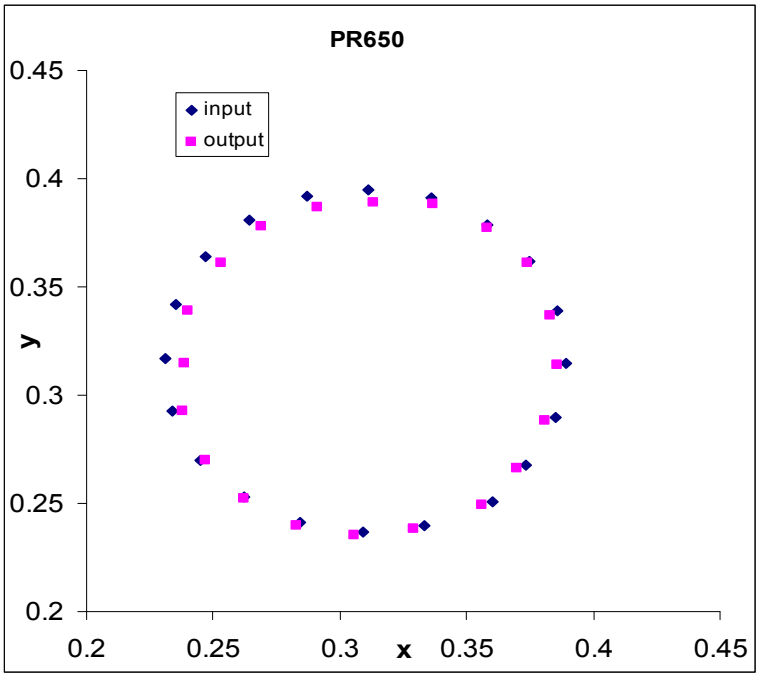


Figure 3.9 Representation of the input- and measured output values in CIE 1931 xy coordinates for 20 hues measured with the PR650 Spectrascan SpectraColorimeter. The CIE 1931 xy values of the tested coordinates are displayed in **Table 3.1**. Y = 12.5 cd/m^2.

3.3 Spatial Frequency Stimuli

3.3.1 Stimulus Presentation

Sinusoidal grating stimuli were displayed as described in **Section 3.2.1**, using the same stimulus display, background colour and luminance, viewing conditions and software.

3.3.2 Stimulus Configuration

Sinusoidal luminance and chromatic contrast gratings were employed as stimuli. The reference, mask and test stimuli were presented in circular windows of diameter equal to 2.5° of visual angle, on a 12.5 cd/m^2 equiluminant background of illuminant C (CIE co-ordinates: x = 0.310, y = 0.316) (see **Figure 3.10**). The contrast of the reference and test stimuli was set to 50%. In the different experiments the reference stimulus was set to one of three different spatial frequencies (1, 3, 5 c/deg) and test spatial frequencies fell within a range above and below the reference spatial frequency, in seven equal steps including one of the reference spatial frequencies. This range was individually adjusted for each observer in order to acquire a smooth psychometric function.

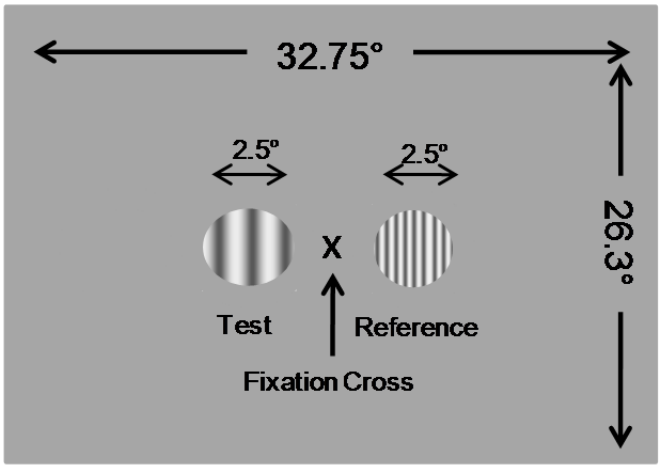


Figure 3.10 The stimulus configuration in the spatial frequency experiments. See detailed explanation in the text.

Contrast was defined by the equation (Michelson contrast), which gives contrast as the difference between the maximum and the minimum luminance, divided by the sum of the maximum and minimum luminance:

$$C = \frac{L_{max} - L_{min}}{L_{max} + L_{min}} \qquad (3.17)$$

The mask stimuli varied in terms of a number of different parameters such as spatial frequency, chromaticity, luminance ratio and contrast (between 10 - 100%). The chromatic content of the stimuli were defined by the 0° - 180° axis of the MBDKL colour space, the CIE 1931 xy coordinates of the two colours were; red (x = 0.3819; y = 0.2826), green (x = 0.2381; y = 0.3494).

Luminance content of the chromatic stimuli was changed by varying the luminance ratios of the constituent chromaticities:

$$L = \frac{L_{\lambda R}}{L_{\lambda R} + L_{\lambda G}} \tag{3.18}$$

Where, $L_{\lambda R}$ and $L_{\lambda G}$ are luminance values of the composing chromaticities of the chromatic grating. Luminance ratios ranged between 0 and 1, where values of 0 and 1 yield entirely luminance defined stimuli, and a ratio of 0.5 defines an isoluminant chromatic grating, which contains only chromatic contrast (photometric isoluminance point). Other values result in stimuli of varying chromatic and luminance content (**Figure 3.11**) (McKeefry & Burton, 2009; Mullen & Baker, 1985).

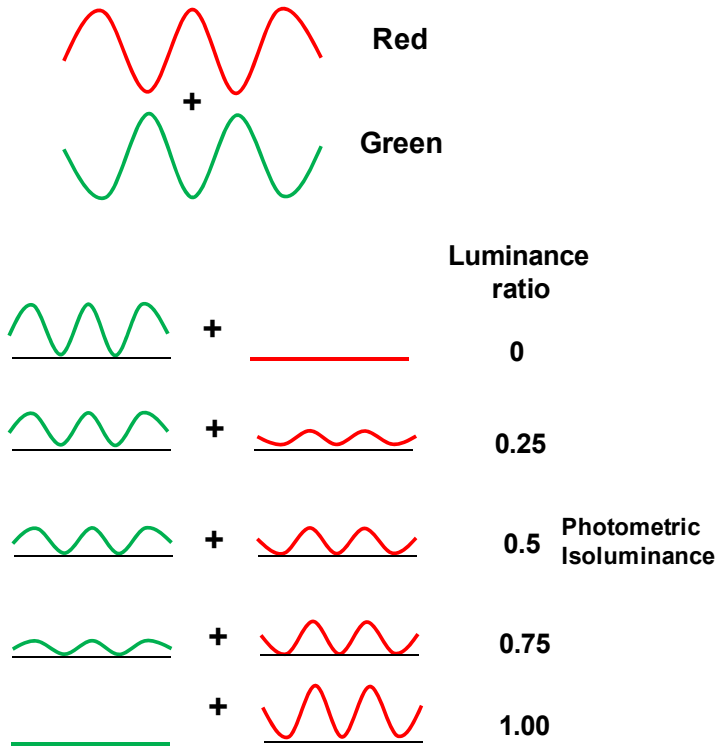


Figure 3.11 Luminance profiles of coloured stimuli in a red-green sinusoidal grating. Isoluminant stimuli is defined by a luminance ratio of 0.5 (i.e. indicates the condition when the stimulus contains chromatic contrast only), and increasing and decreasing luminance ratios define stimuli of varying chromatic and luminance content as illustrated on the figure (Modified after: (Mullen & Baker, 1985)).

3.3.3 Monitor Calibration

There is a nonlinear relationship between the entered digital inputs to the frame buffer (voltage) and the intensity of the emitted light (output), this is called the gamma function (**Figure 3.12**). In order to ensure a linear relationship, calibration of luminance and correction of colour values have to be implemented.

$$L = k\left(V - V_0\right)^{\gamma} \tag{3.19}$$

Where, V = applied voltage, V_0 = brightness level, γ = 2.5 and k = constant.

Colour and luminance calibration of the monitor was performed with ColourCAL colorimeter (Cambridge Research Systems Ltd., Rochester, UK), and the PR-650 SpectraScan Colorimeter (Photo Research Inc., Chatsworth, California,

USA). The stimuli used for calibration were the ones that were provided with the software. The calibration was carried out in a dark room. At first, monitor luminance output as a function of increasing voltage - called the gamma function - was measured by introducing a gray scale. After this, the software set the frame buffer entries for the three different monitor phosphor values, and the monitor output values were measured at different luminance levels with the PR-650 SpectraScan Colorimeter. The frame buffer entry of one phosphor was set to a value, the photometer measured the intensity of the emitted light and repeated this measurement for many entry values in case of all three phosphors. Based on the measurements calibration curves (gamma curves) for the R, G and B phosphors (three chromatic guns) were plotted. The RGB values were converted to CIE 1931 xy chromaticity coordinates by the calibration software. The input voltage values (x, y, Y input levels) were then altered based on Look-Up Tables (LUTs) so that the output values resulted in a linear function. The original voltage values for R, G and B were divided by the adjusted value, which gave the correction factors for the three phosphors that we used in the final calibration.

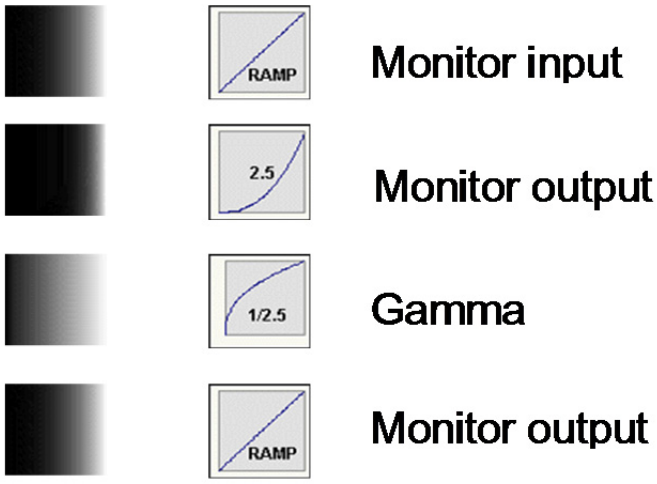


Figure 3.12 Schematic example of simple gamma correction. Monitors have a nonlinear relationship between the voltage inputs and the intensity of the emitted light (luminance). This nonlinearity is described by a power function, called gamma (in this example gamma = 2.5). In order to account for this nonlinear relationship, the entered voltage values are raised to the power of 1/2.5 (CGSD Corp. (n.d.) [Online Image] Available at: <http://www.cgsd.com/papers/gamma_intro.html> [Accessed 23 March 2010]).

3.4 Motion Stimuli

3.4.1 Stimulus Presentation

Moving sinusoidal grating stimuli were presented as described in the previous section, using the same stimulus display, background colour and luminance, viewing conditions and software, for details see **Section 3.2.1**.

3.4.2 Stimulus Configuration

The motion stimuli consisted of vertically oriented luminance and chromatic gratings that were presented in a square window that had a size of 2.5° in the centre of the screen on an equiluminant grey background (illuminant C) that had a mean luminance of 12.5 cd/m^2 (CIE coordinates: x = 0.310, y = 0.316) (**Figure 3.13**). The gratings moved with a given velocity defined by the temporal frequency divided by its spatial frequency (speed = ft/fx). The temporal frequency was changed accordingly while the spatial frequency was set to 1 c/deg. The reference velocity was set to 3 or 6 deg/s and the test stimuli corresponded with seven velocities within a range of approximately ±40%, the step size was adjusted to the discrimination ability of the individual, in order to acquire a gradually changing psychometric function. The contrast of the reference and test stimuli was set to 50% (approximately 10x motion detection threshold), and was varied randomly across ±5% to prevent the build-up of long term representations. These variations were balanced over the trials in order to minimise any bias (Magnussen & Greenlee, 1992). The direction of the moving gratings was also varied to prevent learning.

The mask stimuli were changed in terms of velocity and chromaticity in the different experiments. The chromaticities of the stimuli were varied along the axes of MBDKL colour space. L, M and S-cone modulations represented changes along the azimuth (ϕ) on the equiluminant plane. The hues of the masking stimuli represented the 0° - 180°, or L - M axis of modulation in MBDKL colour space (CIE chromaticity coordinates: x_0 = 0.3819, y_0 = 0.2826; x_{180} = 0.238, y_{180} = 0.3494). The luminance contrast of the stimuli was varied along the Θ axis, between 0° (equiluminant plane) and ±90° (purely achromatic contrast) (Derrington et al., 1984; McKeefry et al., 2006).

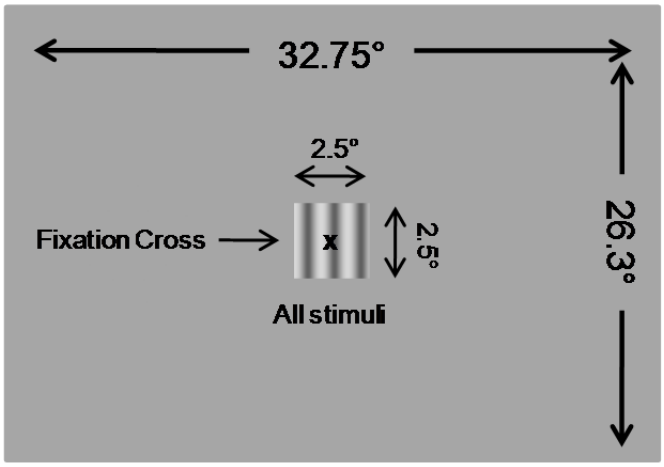


Figure 3.13 Illustration of the stimulus display during the motion experiments. See detailed explanation in text.

3.5 Psychophysical Techniques

3.5.1 Introduction

Psychophysical experiments employ physical stimuli the attributes of which can be easily and objectively adjusted and measured, and the consequent effects on perception and task related behaviour of the observers can be measured. In vision science, psychophysics enables the examination of sensory processing,

namely, the sensitivity of the visual system to detect the presence and changes of stimuli.

3.5.2 The Psychometric Function

The performance of an observer in a psychophysical experiment, namely the relation between the performance and the physical properties of the stimulus is described by the psychometric function. It describes the relationship between the physical characteristics of a stimulus and the response of the observer. The percent of 'yes' responses ('seen', or 'different', depending on the task) is plotted as a function of the examined stimulus dimension. The resulting psychometric function, or in other words; frequency-of-seeing curve is of sigmoidal shape, the 'y' axis presents the percentage of correct answers and 'x' axis depicts the examined stimulus parameter (**Figure 3.14**). The stimulus values (on the x axis) for both the absolute and discrimination thresholds are identified by their location on the y axis on the curve where the observer notices the presence of a stimulus or the difference between two stimuli 50% of the time (Carpenter & Robson, 1999).

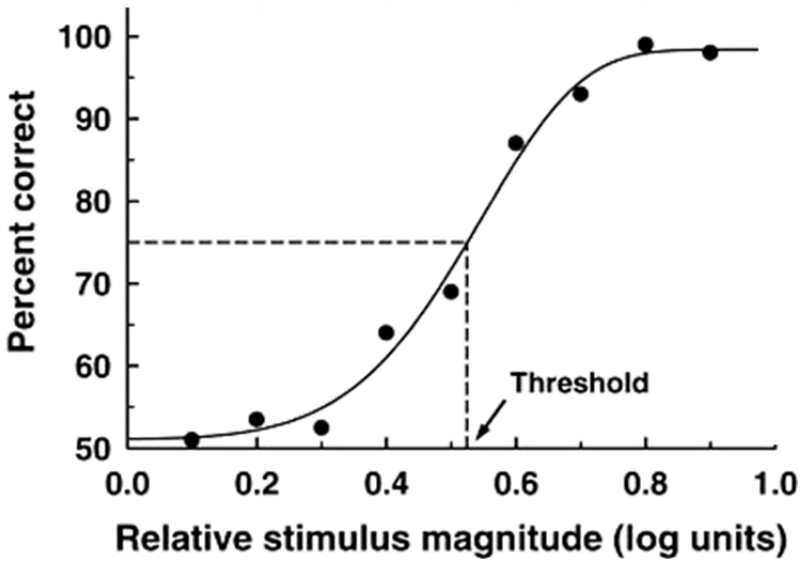


Figure 3.14 Example of fitting of logistic function to the raw psychometric data. PSE values indicate 50% correct response level, and discrimination thresholds indicate the rate of the decay of the curves, namely, the difference the reference and test have to have in terms of a certain stimulus attribute in order to be perceived as different. (MITCogNet (n.d) [Online Image] Available at: <https://cognet.mit.edu/login/?return_url=%2Flibrary%2Ferefs%2Fheckenlively%2Fc026%2Fsection1.html> [Accessed 25 August 2010].

3.5.3 Measures of Performance

There are different measures that can be obtained from the experimental data in order to quantify performance. Threshold refers to a given stimulus intensity that is required in order to achieve a given preset performance (Pelli & Farell, 1995). In vision science, the absolute threshold is measured in detection tasks and provides information about the intensity level of the just detectable stimulus that is required in order to be seen by the observer. Discrimination threshold experiments measure difference thresholds, which refer to the amplitude of the difference that is needed between two detectable stimuli in terms of a given stimulus characteristics in order for them to be perceived as being different.

The Point of Subjective Equality (PSE) is another useful measure of performance; it gives information about the required shift in a certain stimulus

dimension that is needed in order for the observer to perceive the two stimuli as being equal.

3.5.4 Method of Constant Stimuli

In this experimental design, a small fixed number of different stimulus intensity levels (5 - 9 around threshold) are chosen by the experimenter, and each of them are presented multiple times in a random order, to determine the frequency of perceived stimuli and the psychometric curve (frequency of seeing curve). The reference stimulus has a constant intensity and the test intensities vary within a fixed range. Discrimination threshold has been used as an indicator of performance and it is identified at 50% correct response level. In general the subject in this experimental design is not able to predict the next stimulus level; therefore there is less chance of an error due to habituation and expectation.

The ‘yes/no’ procedure is mostly used in order to determine absolute threshold levels; observer responds ‘yes’ if the stimulus is seen and ‘no’ if it is not seen. The absolute threshold is set at 50% correct response stimulus intensity level detected as seen (‘x’ axis: stimulus intensity, ‘y’ axis: proportion of detected responses) (Gescheider, 1985). In order to measure difference thresholds, reference and test stimuli are presented and the observer makes a comparison between the two stimuli in terms of the examined attribute. In this case stimulus value of 0.5 on the psychometric curve refers to the point of subjective equality whereas values of 0.25 and 0.75 locate difference thresholds (Gescheider, 1985). Modifications of this method were later on introduced to address the problem that arises when many of the test stimulus intensities are well above or below threshold. These values do not give valuable information about the

observers' performance. To decrease the duration of the experiment the reference stimulus can be omitted because observers can make comparisons without being constantly presented with the reference based on subjective standard after previous experience.

3.5.5 Forced Choice Procedure

In a two-alternative forced-choice procedure, the observer is constrained to choose between two alternatives, which counteracts the effect of response bias and guessing. The subjective observer criterion is removed by displaying the stimulus in a spatially or temporally separated manner and the observer has to indicate in which interval the stimulus was displayed (Blackwell, 1953). Decisions have to be made independently of detectability, which means that the observers are forced to make a decision, even in the case when they are uncertain whether they see a stimulus or not. The procedure can be combined with the method of constant stimuli, in which a fixed set of stimuli are presented in one of two spatial or temporal positions. In our experiments the stimuli were temporally and/or spatially separated and the observers had to indicate the direction of the difference of the test stimuli compared to the reference in terms of the examined stimulus dimension.

The percentage of correct responses is plotted as a function of stimulus intensity. The 50% correct level represents the guessing rate, which is considered to be the worst performance in this case and threshold is defined as the stimulus intensity where 75% of the answers are correct. This method has proved that observers can discriminate stimuli that are below threshold based on subjective methods. This objective method is very useful to rule out individual criterion factors or sensory differences. The forced choice procedure

can also be carried out in a staircase design, and all of the subjective methods can be converted into a forced choice procedure. The staircase procedure is a fully automated modification of the forced choice procedure that was developed to explore and measure the threshold point of the psychometric curve. In this case, the stimuli are presented and if the observer responds correctly on three trials the stimulus intensity is decreased whereas if the answers are incorrect on three successive trials the stimulus intensity is increased. Threshold level is defined at 79% correct level.

3.6 Experimental Procedures

3.6.1 Colour Experiments

3.6.1.1 Hue Scaling

A hue naming procedure was performed in preliminary experiments. The experiment involved the scaling of a range of isoluminant colours into the four basic colour categories; red, blue, green and yellow, to generate colour naming functions (p[colour]) (see **Chapter 4**, **Section 4.2**).

Stimuli were defined in CIE xy (1931) colour space based on the 2° standard observer (**Table 3.1**) and expressed as vectors in the modified MBDKL chromaticity diagram (**Figure 3.5**) (MacLeod-Boynton chromaticity diagram described by Derrington et al.) (Derrington et al., 1984; Krauskopf et al., 1982). The stimuli consisted of 20 circular, hard edged coloured patches with a diameter of 3°, and the chromaticities (saturation) were given as equal length vectors that formed a circle equally spaced around the white point in steps of ϕ = 18° ranging from ϕ = 0° to ϕ = 360° on an isoluminant plane (Y = 12.5 cd/m^2) (**Figure 3.15**). The background was a uniform grey of luminance equal to 12.5

cd/m^2 defined as the white point (CIE 1931 chromaticity coordinates; x = 0.310, y = 0.316, illuminant C). Stimulus chromaticity coordinates (CIE 1931 xy) are shown in **Table 3.1**.

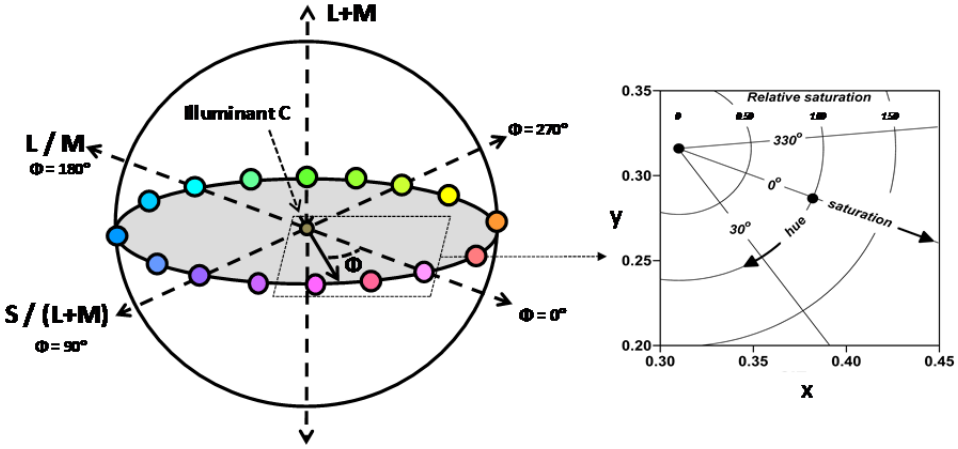


Figure 3.15 The MBDKL colour space showing a section of the isoluminant plane in order to illustrate the direction of changes in colour space, as hue and saturation is changed by means of vector rotation or vector length, respectively. The concentric circles denote baseline saturation levels as well as higher and lower ones. For example, on this illustration, the changes in saturation of axis 0° are highlighted.

In a four-alternative forced choice experimental design (De Valois et al., 1997b; Parry et al., 2006) observers were presented with each of the 20 different hues 20 times in a random order and observers indicated by a CB3 response box, whether the presented colour stimuli appeared blue, green, yellow or red. Stimuli were circular, sharp edged patches the diameter of which subtended 3° of visual angle, and were presented on the centre of the monitor for 380 ms. The following stimulus was presented 250 ms after the observer made a response (**Figure 3.16**). There were altogether 400 stimulus presentations during the course of this experiment. The experiments were performed in a darkened room, usually allowing 10 min for dark adaptation, and 5 min of adaptation to the background illuminant. Observers fixated on a small black fixation mark on the centre of the screen binocularly from a 114 cm viewing distance.

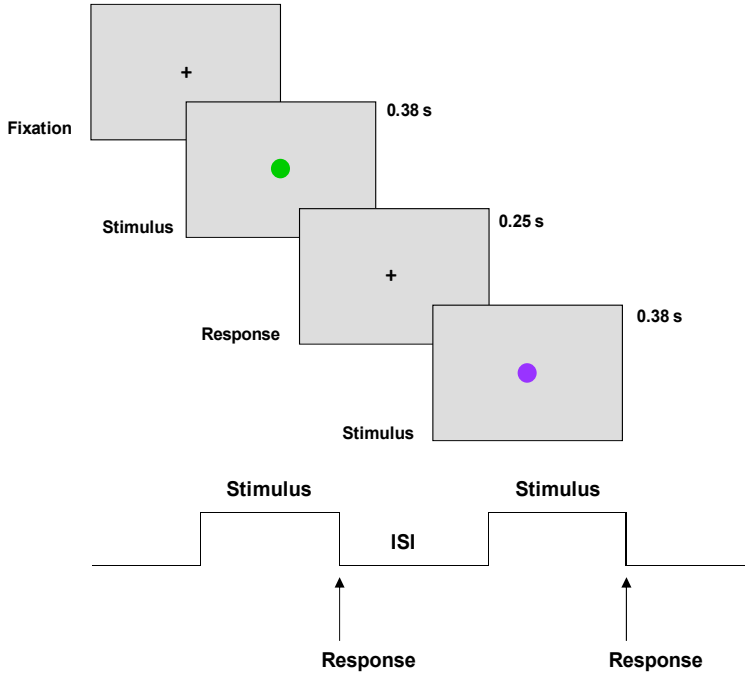


Figure 3.16 Schematic of the colour naming experiment. The observer fixates at the centre of the screen and makes a response after the presentation of the stimulus. The subsequent stimulus appears following the response. Any of the 20 different hues can appear in the centre of the screen and the available response options are Red, Green, Blue and Yellow.

Five observers took part in this experiment (3 females, 2 males; mean age ±1 SD, 36.2 ± 5.6 years). All had normal colour vision according to Rayleigh matches made on a HMC Anomaloskop (Heidelberg) and the Farnsworth-Munsell 100-Hue test. All had 6/6 or corrected to 6/6 Snellen visual acuity.

The results were analyzed by deriving four colour naming functions: p[red], p[blue], p[green] and p[yellow], where p[colour] was the proportion of times that a particular test hue was called that colour out of a total of 20 presentations (Parry et al., 2006). 12 colour stimuli for each observer were located based on the data (**Figure 3.17**). Exemplars of the four unique hues (red, blue, green and yellow) were defined as the central maxima of the hue scaling functions. The four 'cross-over hues' corresponded to the axes in colour space where the presented stimuli were equally likely to be identified by adjacent colour appearance mechanisms (R-B, B-G, G-Y and Y-R) and the four 'cardinal hues' represented axes that isolate the activity of cone opponent mechanisms (ϕ = 0° - 180°, ϕ = 90° - 270°).

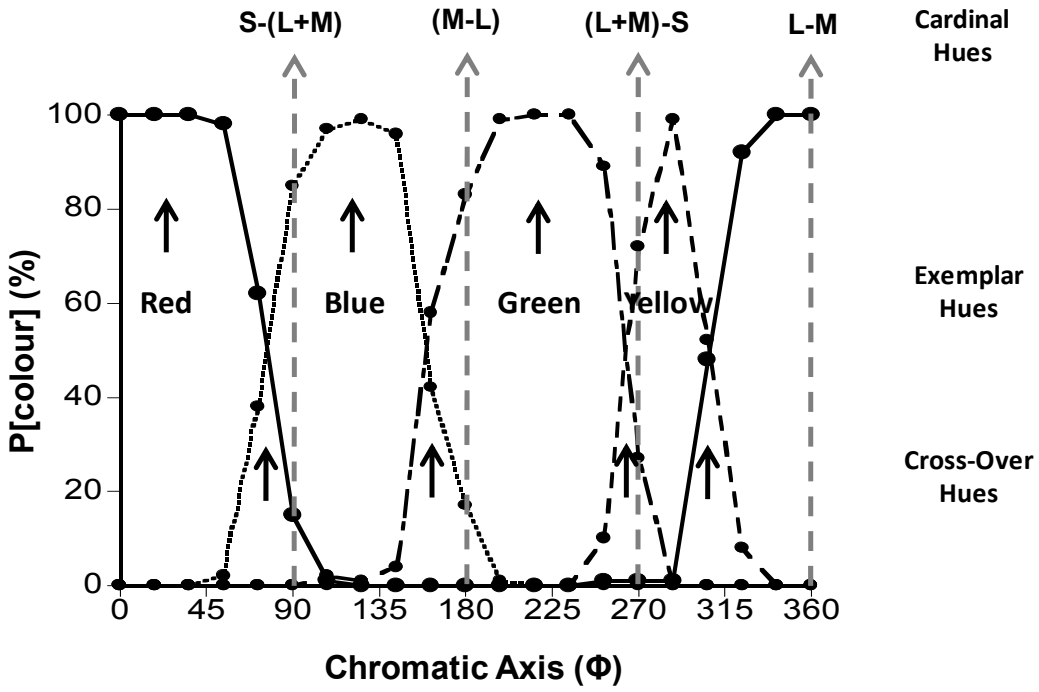


Figure 3.17 Example of hue scaling functions showing the chromatic axes in MBDKL colour space. The hue naming functions are expressed as percentages (p[colour](%)) and plotted as a function of chromatic axis. Dashed grey vertical lines represent the cone opponent mechanisms and the short black arrows point to the perceptual colour categories, namely the Exemplar and the Cross-Over Hues.

3.6.1.2 Delayed Colour Discrimination

In these experiments we examined colour memory for up to 10 s delays in case of 12 preset colours (**Chapter 4**). The experiments involved the presentation of a chromatic reference stimulus chosen from any of one of the 12 orientations in colour space employing a delayed matching paradigm, following the hue scaling experiment (**Figures 3.16 and 3.17**) (Magnussen & Greenlee, 1999; Magnussen et al., 2003). The 12 reference hues consisted of four intermediary, four unique hues and the four hues that represented the cardinal axes of the cone opponent mechanisms (**Table 3.2**).

The stimuli consisted of pairs of coloured circular hard edged patches and their diameter subtended 1.5° of visual angle. As described before (see **Section 3.6.1.1**), the colour stimuli were specified as equal length vectors in MBDKL colour space by their angle of rotation (ϕ) on the isoluminant plane (**Figure 3.15**)

(Derrington et al., 1984; Krauskopf et al., 1982). The background was a uniform grey of luminance equal to 12.5 cd/m^2, defined as the white point (illuminant C, CIE 1931 xy chromaticity coordinates; x = 0.310, y = 0.316,). The chromaticities of the test stimuli were within a predefined range of ϕ = -20° - +20°, relative to the reference colour. They were generated by clock- and anticlockwise vector rotation relative to the reference hue in steps of ϕ = 3° or 4°. This resulted in 11 test stimuli for each reference colour. **Figure 3.18a** shows an illustration of an ϕ = 18° reference and corresponding test stimuli. As can be seen on the figure, the two extreme colours of this range were easily discriminated from the reference.

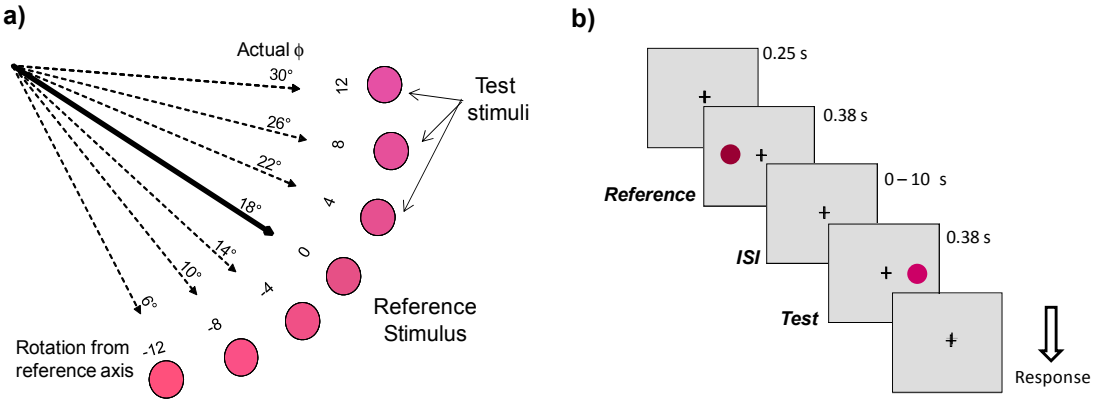


Figure 3.18 Stimulus design and paradigm. a) Illustration of an exemplar reference axis and corresponding test stimuli for test stimulus rotations between ϕ = -12° and +12° in case of a reference colour of ϕ = 18. b) Delayed match to sample paradigm. Observers fixated at the centre of the screen and reference stimuli appeared on the left of the fixation mark for 0.38 s. Test stimuli appeared on the right side of the fixation, simultaneously and with 1, 5, 10 s delays. Observers were asked to decide whether the two colours were the same or different.

Table 3.2 Localisation of exemplar hues based on the colour naming curves for five colour normal observers. The location was the central maxima of the colour matching function. These exemplar hues served as reference axes in the experiments.

OSERVER	RED	BLUE	GREEN	YELLOW
DM	18°	126°	202°	279°
VN	18°	117°	207°	279°
JH	18°	117°	225°	288°
UT	18°	126°	234°	288°
CL	18°	117°	225°	288°

In a delayed match-to-sample paradigm, the reference and test stimuli were presented simultaneously and successively with 1, 5 and 10 s Inter Stimulus Intervals (ISI) in the different runs. In each run, four of the reference stimuli were intermixed and presented in pairs with their corresponding test stimulus range (**Figure 3.18**). The reference stimuli were presented 1.5° away from the central fixation point on the right side along a horizontal plane, and the test stimuli were presented on the left side at the same distance along the horizontal plane, while the observers fixated on the centre of the screen (**Figure 3.18**). Each stimulus was presented for 380 ms and the reference stimulus appeared 250 ms after the observer made a response. In order to minimise rehearsal effects, which would be generated by repeated exposures to the same stimulus, the reference was varied from trial to trial, therefore the observer could not predict which stimulus had to be matched on consecutive trials. Typically, four different reference hues and their corresponding test stimuli were combined in a random order in a multiple probe design. Every single reference and test pair was presented 10 times. Since there were 11 different test hues for every reference stimulus, and each test hue was presented 10 times in a random order, there were 110 presentations and consequent answers during each run. Each run lasted for approximately 30 - 180 min, and every observer completed approximately 20 experimental runs. Simultaneous colour matching performance served as baseline, where the test and the reference appeared on the monitor at the same time and observers had to simultaneously discriminate them.

The experiments were performed in a darkened room, usually allowing 10 min for dark adaptation. Observers fixated on a small black fixation mark on the centre of the screen binocularly from a 114 cm viewing distance. The task of the

observer was to indicate with an appropriate button press whether the presented test stimulus was the same or different from the reference (CB3 response box, Cambridge Research Systems).

The same five observers took part in this study (3 females, 2 males; mean age ±1 SD, 36.2 ±5.6 years) as in case of the hue naming experiments. All had normal colour vision according to Rayleigh matches made on a HMC Anomaloskop (Heidelberg) and the Farnsworth-Munsell 100-Hue test. All had 6/6 or corrected to 6/6 visual acuity as tested with the Snellen chart.

3.6.1.3 Colour Memory Masking

In these experiments we employed masking stimuli in order to examine stimulus selectivity for colour in VSTM (see **Chapter 5**). All stimuli were circular, had sharp edges, subtended 1.5° diameter of visual angle and were presented on an equiluminant grey background that had a luminance of 12.5 cd/m^2 (CIE coordinates: x = 0.310, y = 0.316). Reference colours were the four typical representations of unique hues which were identified in the previously described hue scaling experiment. **Table 3.2** shows the individual locations of the four exemplar hues expressed as angles of rotation in MBDKL colour space. Seven isoluminant, equally saturated test hues represented a range equally sampled within $\phi = \pm 21°$ on each side of the axis of the reference in steps of $\phi = 7°$ (**Figure 3.19**). The two endpoints were easily discriminable from the reference, one of the tests had the same hue and the rest were of different difficulties in terms of discriminability (**Figure 3.19**).

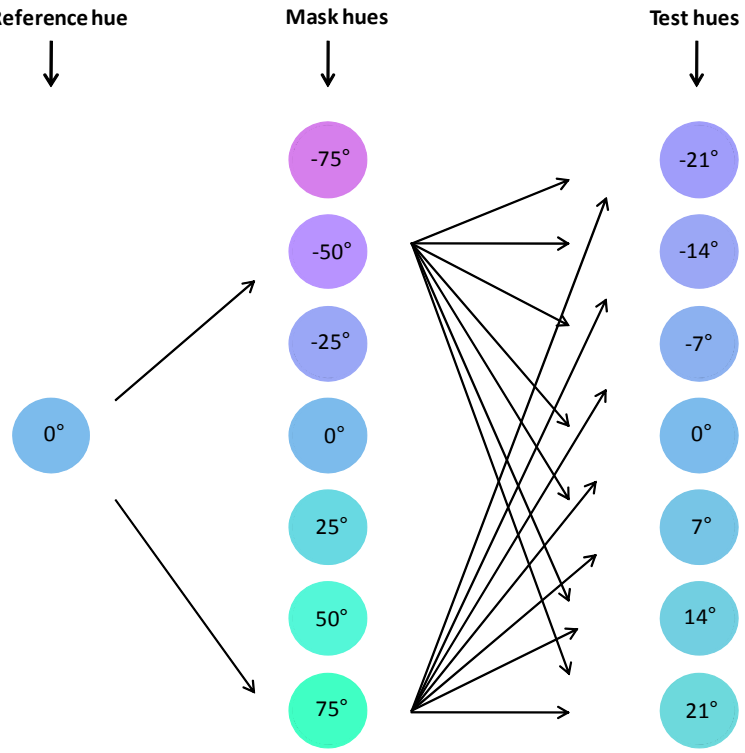


Figure 3.19 Schematic representation of the employed stimulus hues. See detailed explanation in the text.

In a delayed match-to-sample paradigm in conjunction with a method of constant stimuli, the reference stimulus was presented and followed by the ISI before the test stimulus appeared (**Figure 3.20**). The reference and test stimuli were presented for 380 ms and the ISI was set to 5 s. Stimuli were displayed in a spatially separated fashion in order to eliminate possible retinal adaptation and chromatic induction effects. The reference and test appeared 1.5° either side of a central fixation mark along a horizontal line and were temporally separated by an ISI=5 s. The different stimulus properties of the mask stimuli such as onset, duration and hue were changed accordingly during the experiments (**Figure 3.20**). These details are described in the individual sections in **Chapter 5**. The no mask condition served as baseline and in forthcoming trials the mask stimulus was introduced during the ISI. The reference appeared to the right, the mask on the fixation mark in the centre and the test on the left side of it. All runs were repeated at least two times to

facilitate competent implementation of the task. Observers were required to fixate on the central fixation mark and indicate towards which adjoining colour category the test stimulus was located via the response box after the test stimulus presentation (**Table 3.3**).

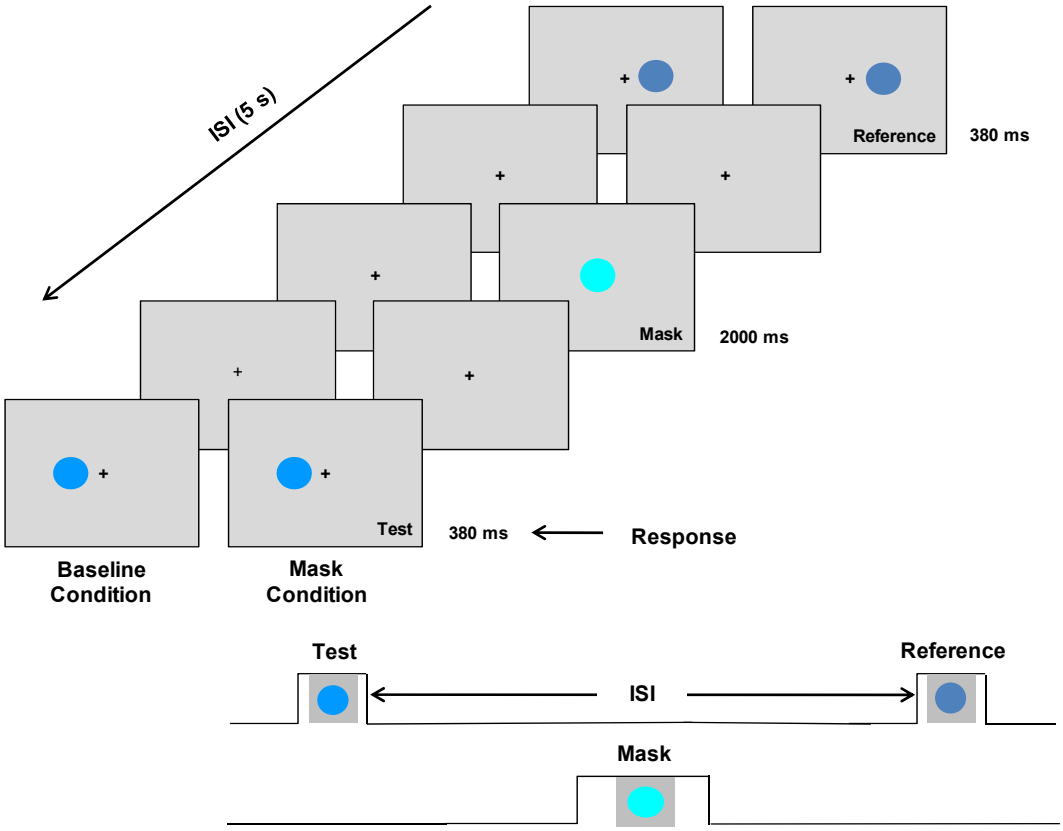


Figure 3.20 Schematic representation of the delayed match to sample paradigm in conjunction with the method of constant stimuli. The hue, saturation and luminance level of the mask could be varied in the different runs. In all cases the observer was required to decide towards which adjoining colour category the test stimulus changed compared to the reference.

Table 3.3 Colours that represent clockwise or anticlockwise rotations in MBDKL colour space in relation to the reference hues.

CLOCKWISE (+ 21°)	REFERENCE	ANTICLOCKWISE (- 21°)
Green	Blue	Red
Blue	Red	Yellow
Red	Yellow	Green
Yellow	Green	Blue

Altogether five observers took part in this study (2 females, 3 males; mean age ± 1 SD = 37.4 ± 12.56). All had normal colour vision according to Rayleigh matches made on a HMC Anomaloskop (Heidelberg) and the Farnsworth-

Munsell 100-Hue test. All had 6/6 or corrected to 6/6 visual acuity as tested with the Snellen chart.

3.6.2 Spatial Frequency Memory Masking

In these experiments we examined selectivity for spatial frequency in VSTM employing masks of different physical parameters (see **Chapter 6**). Stimuli of sinusoidal luminance contrast gratings were presented on a 12.5 cd/m^2 equiluminant grey background of illuminant C (CIE co-ordinates: x = 0.310, y = 0.316). The stimuli appeared in circular windows of 8° diameter. Reference spatial frequencies were set to 1, 3 and 5 c/deg in the different runs and the corresponding seven equal steps of test spatial frequencies ranged $\pm$ 2 octaves around the actual reference spatial frequency. Luminance mask stimuli of various spatial frequencies, contrasts and orientations were employed in separate runs. In order to prevent the representation of stimulus features being built up in long-term memory over consecutive trials, we introduced small random increases and decreases in the contrast (between $\pm$ 10%) and spatial phase (between $\pm$ 90°) of the test and reference stimuli. These variations were balanced over the trials to minimise any bias (Magnussen & Greenlee, 1992).

A delayed spatial frequency matching paradigm (**Figure 3.21**) was used to measure performance and employed a two-alternative forced choice procedure in conjunction with a method of constant stimuli. Each trial began with the presentation of a reference of a given spatial frequency (typically 1, 3 or 5 c/deg), which was presented for 380 ms. This was followed by an ISI of typically 5 s, during which masking stimuli were presented. At the end of the ISI a test stimulus was presented for 380 ms the spatial frequency of which was changed randomly within the predefined range. The offset of the stimulus was marked by

an auditory cue at which point the participants were required to indicate, using the response box (model CB3; Cambridge Research Systems), whether the test stimulus was perceived to be of higher or lower spatial frequency than the reference.

There were two versions of the experiment; in the spatially coincident condition, reference, test and mask stimuli were presented on the centre of the screen in the same location, centred on the fixation point, while in the spatially non-coincident condition, stimuli appeared in different locations in the visual field along a horizontal axis (i.e. reference to the right, test to the left of the fixation mark and mask in the centre with no overlap in the location). The magnitude of the displacements from the fixation point varied up to a maximum of 6° (see further details in **Chapter 6**).

A single run consisted of ten repetitions of each stimulus presentation (i.e. each pair of reference and test stimulus) for the seven test stimuli resulting in altogether 70 presentations of reference-test pairs and subsequent responses in a randomized manner. Each run was repeated three times.

Observers were required to fixate at the centre of the screen where a fixation mark was provided. Observers were positioned 114 cm from the display in a darkened room in a headrest and viewed the stimuli binocularly. Responses were recorded via a response box (model CB3; Cambridge Research Systems).

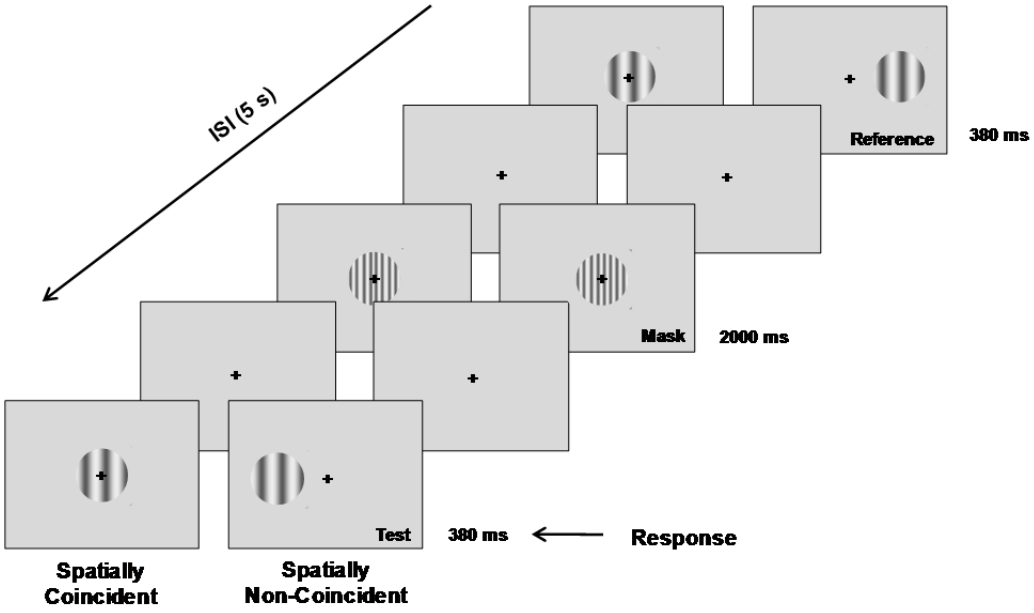


Figure 3.21 A schematic representation of the delayed spatial frequency discrimination paradigm used throughout these studies. Each cycle began with the presentation of a reference stimulus (1, 3 or 5 c/deg) for 380 ms. Following the presentation of a blank screen for different intervals a mask stimulus was displayed for various durations. After another presentation of a blank screen a test stimulus was presented and at the offset of this stimulus the observer was instructed to respond by a button press, indicating whether they judged the test to be of higher or lower spatial frequency than the reference stimulus. Following the response the next presentation cycle began. There were two forms of the experiment; a spatially coincident version, in which case the reference, test and mask stimuli were all presented at the same spatial location centred on the fixation point, and a spatially non-coincident version, where the stimuli were horizontally displaced form one another by separations of up to 6°.

3.6.3 Motion Memory Masking

In these experiments stimulus selectivity for motion, luminance and colour information in VSTM was examined (see **Chapter 7**). Vertically oriented drifting sinusoid gratings served as stimuli, which were presented in a square window of 2.5° x 2.5° in the centre of the screen on an equiluminant grey background as before (illuminant C; mean luminance = 12.5 cd/m^2; CIE coordinates: x = 0.310, y = 0.316). The spatial frequency of the gratings was set to a constant 1 c/deg, while the temporal frequency was changed accordingly in the separate experimental runs. The reference velocities were either 3 or 6 deg/s, while the corresponding test velocities represented a range of $\pm$ 2 octaves above and below these velocities in seven equal steps. Luminance and 'red-green' chromatic gratings of different velocity were employed as mask stimuli. The

chromatic grating represented the 0°-180° cardinal axis of MBDKL colour space (CIE 1931 xy coordinates; red (x = 0.3819 y = 0.2826) and green (x = 0.2381 y = 0.3494). Contrast in all cases was set to 50% and was varied randomly across ± 5% to prevent the build up of long term representations. These variations were balanced over the trials in order to minimise any bias (Magnussen & Greenlee, 1992). The direction of the moving gratings was also varied to prevent learning, since it is known that the direction of the moving gratings does not affect the memory for speed.

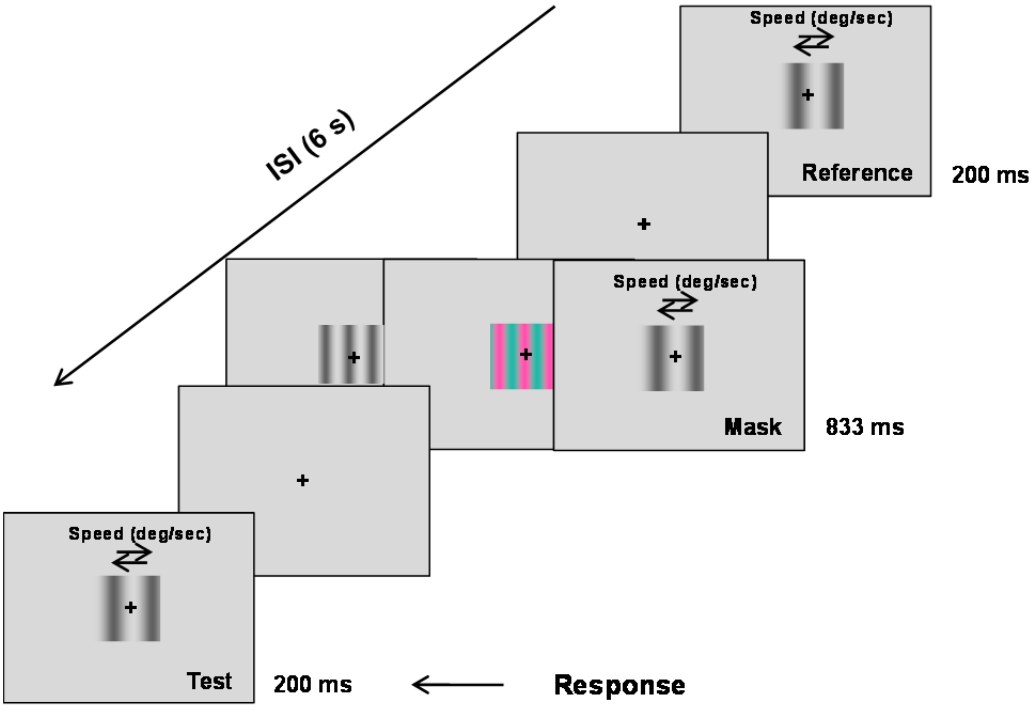


Figure 3.22 A schematic representation of the delayed velocity discrimination paradigm used throughout these studies. Each cycle began with the presentation of a reference stimulus (3 or 6 deg/s) for 200 ms. Following the presentation of a blank screen for different intervals, a mask stimulus was displayed for 833 ms. After another presentation of a blank screen, a test stimulus was presented and at the offset of this stimulus the observer was instructed to respond by button press whether they judged the test to be of higher or lower velocity than the reference stimulus. The stimuli were presented at the centre of the screen while the observer kept his/her gaze on the central fixation mark.

Speed discrimination thresholds and PSE values were determined for the reference and test employing a two-alternative forced choice procedure in conjunction with the method of constant stimuli (**Figure 3.22**). The reference

was set to a constant speed (with a given spatial and temporal frequency) and the corresponding seven test stimuli were presented in a random order. ISI was set to 5 s, reference and test were presented for 200 ms, and mask stimulus was presented for 833 ms. Baseline performance was represented by conditions where no masking stimulus appeared during the ISI. Observers were required to indicate whether the test stimulus was faster or slower than the reference one and communicate their answers via the response box.

As in the previous experiments, observers were positioned at a 114 cm distance and viewed the stimuli binocularly in a darkened room after 10 min of dark adaptation. Observers had normal or corrected to normal visual acuity (6/5) and normal colour vision as tested by the Farnsworth-Munsell 100 Hue test and a mean age of 38 years (1 female, 1 male).

3.7 Data analysis

3.7.1 Least Squares Method

There are different statistical methods to measure the goodness of fit for a psychometric function. The relation between the data and a statistical model gives the concept of fit and the calculation of this fit is called regression. The statistical method that was employed to assess the goodness of fit was the 'least squares' method. The least squares method is a popular choice for curve fitting because it is relatively simple, well understood and it can be fit to a broad range of functions. It can generate a good and efficient evaluation of even small data sets, irrespective of the type of equation that is used with this method. It performs a mathematical calculation to find the best fitting curve, by minimising the sum of the squares of the offsets of the data points. The sum of the squares

of the offsets is used to elicit the problem that arises from summing values of different sign. This method uses data efficiently and can produce good estimates of the unknown parameters in the model, even in case of relatively small data sets. Its disadvantage is that it is sensitive to outliers, therefore the data should always be examined for suitability for fitting since these outliers could result in poor estimation and misinterpretation of the data.

3.7.2 Curve Fitting

In our analysis data were plotted in terms of a percentage of correct matches as a function of changes in the examined stimulus parameter. These data were fitted with Gaussian, logarithmic or first derivative of the Gaussian for qualitative and quantitative evaluation. We used the Kaleidagraph software (version 3.5, GeoMEM Consultants, UK). This program fits the curves and calculates certain important values to describe the results such as the accuracy of the match, discrimination thresholds and perceived shifts as a result of the employed memory delay and stimulus manipulations.

3.7.2.1 Gaussian Curve Fits

Gaussian functions were fitted to the data in the hue scaling and initial colour memory experiments (**Chapter 4**). These were of the form:

$$y = ae^{-\left(\frac{(x-\mu)}{2\sigma}\right)^2} \tag{3.20}$$

Where: *a* is the height of the curve's peak (accuracy of the match), *μ* is the position of the peak in relation to the x-axis (hue shifts) and *σ* is the width or spread of the function (discrimination threshold).

Figure 3.23 shows exemplar matching functions with fitted Gaussian curves obtained for the delayed match to sample task examining the retention of colour information for ISIs = 0, 1, 5 and 10 s for observer VN (see **Chapter 4**). Performance is plotted for a single reference stimulus (azimuth, ϕ = 90°) as a function of the relative rotation of the test chromatic axis away from the reference stimulus, the value 0 on the x-axis indicates that the reference and test are the same.

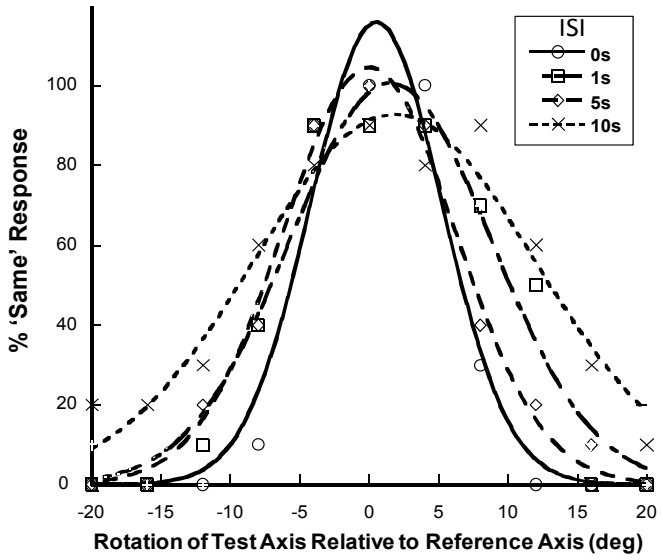


Figure 3.23 Matching functions with fitted Gaussian curves obtained for the delayed match-to-sample task for ISIs = 0, 1, 5 and 10 s for observer VN. Performance is plotted for a single reference stimulus (ϕ = 90°), as a function of the relative rotation of the test chromatic axis away from the reference stimulus. The value '0' on the x-axis indicates the condition when the reference and test are the same.

In the colour memory experiments detailed in **Chapter 4** we examined how *a*, σ and μ changed as a function of ISI. Discrimination threshold provides a measure of the spread of the fitted curve and since it is equivalent to standard deviation, it provided information related to the sensitivity of the match for each colour in the colour memory experiments. The height of the peak of the curve was calculated from the equation as the 'a' value and represented the accuracy of the match, namely, how many times out of the 10 presentations the observer responded as 'the same' to the colours that appeared the same for him/her. M

provides information about the position of the peak of the fitted Gaussian curve. Calculation of the time delay induced shift of these positions in relation to the x axis gives information about the magnitude of perceived hue shift that occurs with increasing time delay between the matched and the actual hue.

3.7.2.2 Logistic Curve Fits

Data from the colour, spatial frequency and motion memory masking experiments described in **Chapters 5**, **6** and **7**, were fitted with a logistic function (Heron et al., 2011). Responses were plotted as '% correct answers' as a function of the changes in terms of the examined stimulus parameter and logistic function was fitted to the matching data:

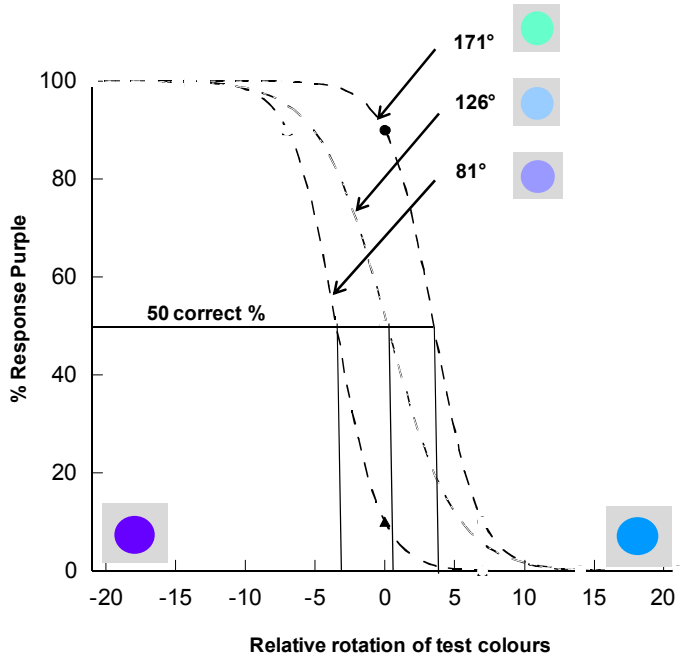
$$y = \frac{100}{1 + e^{\frac{(x-\mu)}{\theta}}} \tag{3.21}$$

Where, - in case of the colour experiments -, *y* is the percentage of times the test was judged the same as the reference, *x* refers to the relative rotation (to the reference) of the test stimulus, *μ* is the matched hue that corresponds to the 50% level on the psychometric function (PSE = point of subjective equality) and *θ* is an approximation of the discrimination threshold. The μ and discrimination threshold values were compared as a function of mask hue to determine the robustness of VSTM for the different visual attributes examined. Examples of these fits are shown in **Figure 3.24**.

Where, - in case of the spatial frequency experiments -, *y* is the percentage of times the test was judged as having higher spatial frequency than the reference, *x* is the spatial frequency of the test stimulus, *μ* is the spatial frequency corresponding to the 50% level on the psychometric function and *θ* is an estimate of the spatial frequency matching threshold. The μ values were

compared as a function of the changes in terms of the examined stimulus attributes.

Where, - in case of the velocity experiments -, *y* is the percentage of times the test was judged as moving faster than the reference, *x* is the speed of the test stimulus, *μ* is the speed corresponding to the 50% level on the psychometric function and *θ* is an estimate of the speed matching threshold. The μ and discrimination threshold values were compared as a function of mask velocity.



3.24 Example of psychometric functions obtained from a delayed hue discrimination experiment. In this experiment the number of times the observer responded 'purple' to a stimulus as opposed to green/turquoise is plotted as a function of the rotation of the test colour in MBDKL colour space relative to the reference colour. The three different psychometric functions here represent data from runs when mask stimuli of different colours (rotation in colour space) were presented during the ISI. The perceived shifts as a result of the different coloured memory masks are located at 50% correct response level on the y axis. The figure illustrates how memory masks of different colours cause a shift in the memory representation of the perceived colour of the reference.

3.7.2.3 First Derivative of the Gaussian Fits

PSE data from the hue masking experiments were fitted by first derivative of a Gaussian functions (Heron et al., 2011) described by the equation:

$$PSE = y_{pos} + \left[\left(\frac{A}{\sigma \cdot e^{-0.5}} \cdot \left(\phi - x_{pos} \right) \right) \cdot e^{-\frac{\left(\phi - x_{pos}\right)^2}{2\sigma^2}} \right] \quad (3.22)$$

Where; *y* is the point of subjective equality (PSE), ϕ is the chromatic axis of the mask relative to the reference in MBDKL colour space, σ is the standard deviation of the Gaussian, *A* is the half amplitude of the function and x_{pos}, y_{pos} is the origin of the function (when $\phi = x_{pos}$, $PSE = y_{pos}$). The maxima and minima of this function occur at mask chromatic axis orientations $\pm\sigma$ units from the origin, i.e. $\phi - x_{pos} = \pm\sigma$. The half amplitude of this function represents the magnitude by which the PSE deviates from baseline (**Figure 3.25**).

In case of the spatial frequency and velocity experiments, the following equation was used:

$$PSE = y_{pos} + \left[\left(A \cdot \log\left(\frac{D}{x_{pos}} \right) \right) \cdot e^{-\left(\frac{\left(\log\left(\frac{D}{x_{pos}} \right) \right)^2}{2\sigma^2} \right)} \right] \quad (3.23)$$

Where y is the point of subjective equality (PSE), *D* is the spatial frequency of the mask, σ is the standard deviation of the Gaussian, *A* is a constant related to the amplitude of the function and, x_{pos}, y_{pos} is the origin of the function (when $D = x_{pos}$, $PSE = y_{pos}$). The maxima and minima of this function occur at mask rotations $\pm\sigma$ units from the origin, i.e. $D/x_{pos} = \pm\sigma$. The half amplitude of this function represents the magnitude by which the PSE deviates from baseline (**Figure 3.25**).

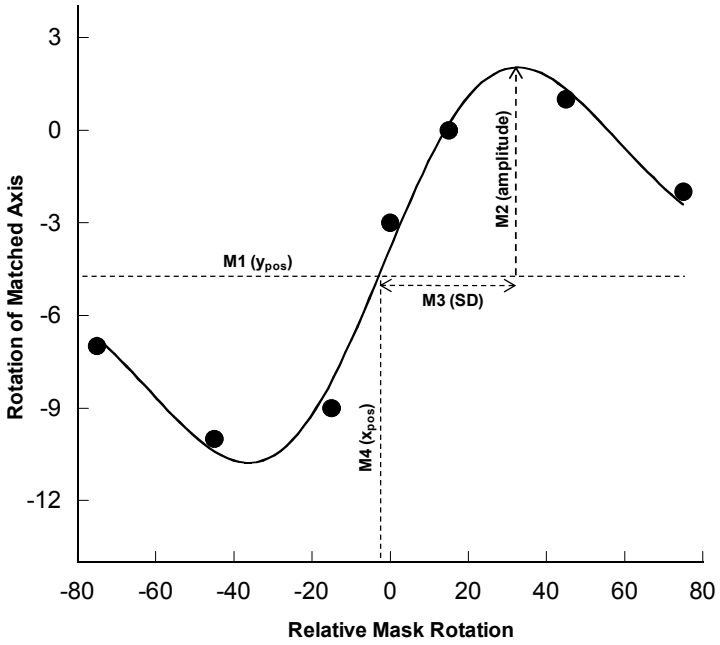


Figure 3.25 Example of 1st Derivative of a Gaussian curve fitted to PSE values and the resulting values that could be extracted from the fitting. M1 values indicate the position of the centre of the curve on the y axis, M4 indicates the position of the centre of the curve on the x axis, M3 refers to the width of the function and M2 gives the amplitude.

3.8 Observers

Detailed observer information can be found in the individual experimental chapters.

3.8.1 Visual Acuity

All observers had normal vision and 6/6 or corrected to 6/6 visual acuity assessed with the Snellen visual acuity chart.

3.8.2 Farnsworth-Munsell 100-Hue Test

The Farnsworth-Munsell 100-Hue Test is a well accepted method of testing colour discrimination ability and ruling out colour deficiencies (Farnsworth, 1957). The test contains 85 chips of equal saturation and brightness out of the 100 hues of the Munsell colour ordering system. The 85 colours of the test are

distributed in four separate boxes, representing a quadrant of the colour circle, in a way that in each box the correct order of the colours result in a gradual shift. The order of the colour chips is mixed during the experiment and under a neutral illuminant the observer is asked to arrange the colours so that their chromaticity changes gradually and they form a uniform sequence of colours. The experimenter then takes a note of the sequence numbers that are on the back of the caps and calculates the scores as a sum of the differences between the adjoining chips. The observer is categorized as having normal discrimination ability if the overall score is below 50. All of the observers who took part in these experiments had superior or average colour discrimination ability, meaning the error score was below 50 in all cases.

3.8.3 Nagel Anomaloskop

The anomaloscope serves for colour vision testing and it is based upon matching a colour by additively mixing two other colours. The Rayleigh equation was used in order to screen for colour defects, where a spectral red light (670 nm) and spectral green light (546 nm) were used in order to match a spectral orange-yellow light (589 nm). The additive mixture of red and green is shown in one part of a bipartite field and the yellow in the other hemi-field. The observer modifies the relative proportions of the spectral red and green lights until he/she perceives the colours of the adjoining hemi-fields as being identical. The types of colour vision defects affect the ability of the observers to make a match. All the observers who took part in the colour memory experiments of **Chapter 4** and **5** had normal colour vision as tested with the Nagel Anomaloskop (Oculus HMC Heidelberg Multi-Color Anomaloskop).

Chapter 4

Behavioural Investigation of Human Visual Short Term Memory for Colour

4.1 Introduction

Studies of VSTM have revealed the existence of a series of parallel, high fidelity mechanisms that are linked to the retention of information relating to specific attributes of a visual stimulus, such as orientation, spatial frequency, velocity and contrast (Greenlee et al., 1991a; Greenlee et al., 1995; Magnussen, 2000; Magnussen & Greenlee, 1992; Magnussen et al., 1991; Magnussen et al., 1985; Nilsson & Nelson, 1981). Colour is another visual dimension that forms an important element of many visual stimuli. Studies have shown that chromatic information can be stored with high degrees of accuracy for fairly long periods of time in short term memory (Bartleson, 1960; Burnham & Clark, 1954; Burnham & Clark, 1955; Newhall et al., 1957; Siple & Springer, 1983). However, when human observers attempt to match a colour from memory there is often a small but measurable decay in performance, which is usually represented by hue, brightness and saturation shifts from the original stimulus (Jin & Shevell, 1996; Newhall et al., 1957; Nilsson & Nelson, 1981). A detailed review of these results is presented in **Chapter 2**, **Section 2.6.2**.

In the distal visual pathway, from the retina to the cortex, colour information is carried by the L-M ('red-green') and S-(L+M) ('blue-yellow') cone-opponent mechanisms, which are distinct from a cone-additive luminance (L+M) mechanism. This segregation of processing within these so-called 'cardinal' mechanisms is kept from the inner retina, via the LGN, to the input layers of the primary visual cortex (V1) (Derrington et al., 1984; Derrington & Lennie, 1984; Hendry & Yoshioka, 1994; Krauskopf et al., 1982). However, there appears to be a transformation away from this cone opponent or cardinal organisation relatively early in the cortical processing of colour. Even though there is evidence for opponent processing in V1 and V2, many neurons here, rather than showing broad chromatic tuning based upon linear cone inputs exhibit narrower chromatic tuning functions, the peaks of which correspond to perceptual colour categories such as red, yellow, green or blue (Conway, 2003; De Valois et al., 2000a; De Valois et al., 1997b; Lennie et al., 1990; Xiao et al., 2007; Xiao et al., 2003). Moreover, according to a recent study by Conway et al. (Conway, 2009; Conway et al., 2007) neurons in the Posterior Inferotemporal Cortex (PIT) appear to be tuned to perceptual colour categories. This suggests that colour processing is re-organised centrally at an early cortical stage and is based around more perceptually relevant, colour appearance mechanisms, as opposed to cone-opponency which predominates in the sub-cortical visual pathway (for a detailed review see **Chapter 1**). The relationship between cone opponent and perceptual colour processing is still obscure, as are the details of this reorganization process.

The purpose of this study was to examine VSTM for colour in view of the aforementioned reorganisation process that takes place between cone opponent and perceptual colour processing. The study intended to examine the

extent to which VSTM for colour is based upon colour appearance categories that have greater perceptual relevance, as opposed to colours which isolate the activity of pre-cortical colour processing mechanisms. This approach is different from earlier ones investigating short term memory for colour, because it also employed key colours that represent the cone opponent mechanisms as well as perceptual colour categories that were identified by a hue scaling procedure (De Valois et al., 1997b; Parry et al., 2006). The difference between the storage characteristics of the two colour categories could highlight the links between perceptual colour processing and storage mechanisms in VSTM. We hypothesised that there would be a better performance in case of perceptual hue categories if memory mechanisms are formed on the basis them. We examined discrimination ability, accuracy of the match and resulting hue shift as measures of performance.

4.2 Hue Naming Experiment

4.2.1 Introduction

Every human with normal colour vision is capable of setting coloured light so that it appears purely green, blue, yellow or red and there will only be minor inter-individual differences in terms of the matches made for these so-called unique hues. This is not the case for any of the other hues which implies that unique hues might have a special significance in the processing of colour (Abramov & Gordon, 1994; Abramov & Gordon, 2005; Boynton & Gordon, 1965).

In the late nineteenth century Ewald Hering (Hering, 1964) observed that the appearance of any colour can be described using solely four basic colour terms,

red, green, blue and yellow, referred to later as ‘unique hues’. Due to the fact that reddish-green and bluish-yellow are non-existent colour sensations he put forward the notion that these colours are perceptually opponent pairs. The four unique hues; red, green, blue and yellow, are defined based on the fact that they appear perceptually unmixed, which means they appear to contain only one colour. They were originally determined by hue cancellation experiments using additive colour mixtures, in which observers were shown mixed colours and were asked to adjust them until they appeared neither red, nor green, or neither blue nor yellow i.e. until equilibrium of these perceptual mechanisms were achieved (Hurvich & Jameson, 1957; Jameson & Hurvich, 1955, 1959). Unique blue and yellow correspond to the equilibrium points of red-green colour opponent mechanisms and unique red and green correspond to the equilibrium points of the blue-yellow mechanism (**Figure 4.1**) (Gordon & Abramov, 1988; Parry et al., 2006). The equilibrium occurs when, for example, there is an orange colour which appears equally yellow and red and the amount of green is increased until the reddishness disappears, which results in unique yellow that does not contain any reddish or greenish component.

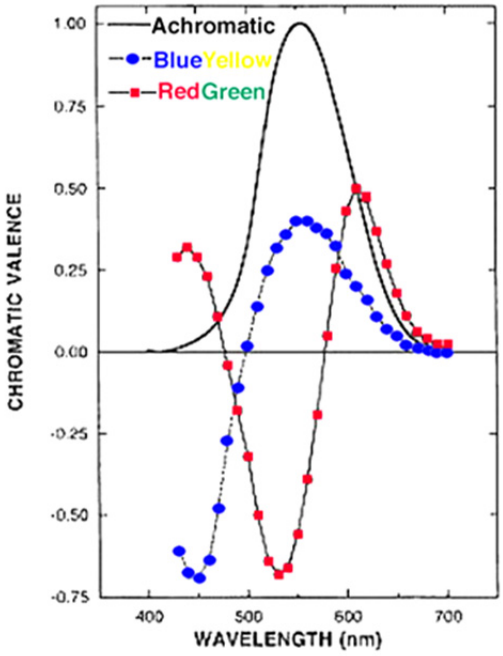


Figure 4.1 Hurvich and Jameson's experiment using blue or yellow and red or green to match all wavelengths of the visible spectrum (Hurvich and Jameson 1957) (Kalloniatis M., Luu C. (n.d.) [Figure15. Hurvich and Jameson experiment using blue or yellow AND red or green to match all wavelengths of the visible spectrum (Hurvich and Jameson's data (1957) from Benjamin, W. J. (Ed), Borish's Clinical Refraction. Philadelphia: W. B. Saunders Company, 1998)] Available at: <http://webvision.med.utah.edu/book/part-viii-gabac-receptors/color-perception/> [Accessed 26 August 2011])

Hue cancellation measurements represent the weighted input of the S, M and L cones into the opponent mechanisms and it was recognized that the hue scaling method can be used in a similar fashion in order to define unique hues (Abramov & Gordon, 1994; Abramov & Gordon, 2005; De Valois et al., 1997b; Gordon & Abramov, 1988; Jameson & Hurvich, 1959; Parry et al., 2006). During a hue scaling procedure, observers are asked to describe presented colours using any combination of the four unique hues. There is a wide range of experiments that have employed different hue scaling methods (Abramov et al., 1992; Boynton et al., 1964; De Valois et al., 1997b) and typically, during these experiments monochromatic lights or coloured patches are presented to the observers, usually in a four-alternative forced choice paradigm and the observer has to classify the presented colour into one of the four colour categories, red, green, blue and yellow.

DeValois et al. (De Valois et al., 1997b) carried out a hue scaling experiment to examine colour naming for isoluminant shifts away from chromatic and white stimuli. One of their aims was to examine hue naming in direct relation to the

degree of activation produced by the LGN opponent cells, therefore they used stimuli that were defined in MBDKL colour space. 16 different isoluminant stimuli, spaced around the opponent axes were used and the observers described each presented colour as a combination of four possible answers of the four different unique colour names. Each presented colour was allowed to be described by a five level scale using exclusively the four basic hue terms. They found that unique hues did not correspond with the cone isolating vectors (i.e. colour opponent mechanisms) that represent colour processing in the sub-cortical pathways, a finding which was in accordance with earlier findings (**Figure 4.2**) (Abramov & Gordon, 1994; Derrington et al., 1984; Krauskopf et al., 1982). They found shifts from the cardinal axes to a variable extent; blue shifted more than yellow, green shifted more than red. The shifts of the unique colours from the axes were consistent with their earlier published multistage colour model (De Valois & De Valois, 1993). Moreover, according to the scaling results the range of colours that fell into each unique category were of varied spread; blue was wider than yellow, red was wider than green (De Valois et al., 1997b).The existence of unique hues serves as a manifestation of the organization of higher order colour processing.

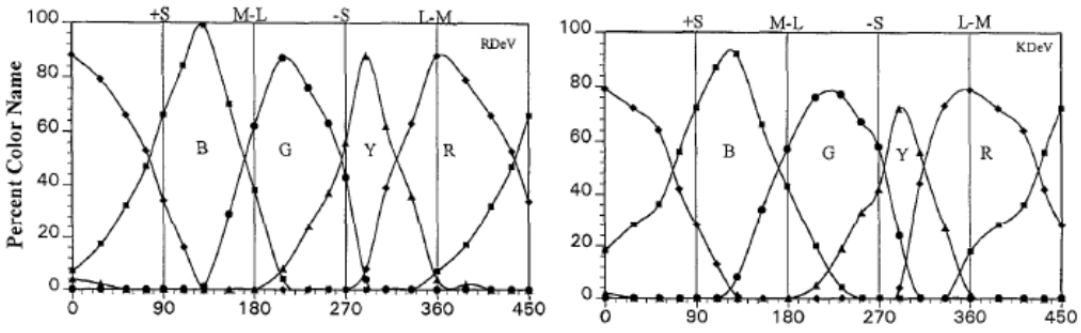


Figure 4.2 Illustration of the results of a hue scaling procedure of isoluminant colours showing individual data from two observers. The percentage of times when a stimulus was scaled into each of the four possible colour categories is plotted as a function of rotation in the employed colour space. The vertical lines indicate the locations of the cardinal axes of MBDKL colour space (De Valois et al., 1997b; Krauskopf et al., 1982) (Source: (De Valois et al., 1997b)).

Several conclusions were drawn from these experiments. First of all, that any colour can be categorized using only the four basic hue terms and even when a weighted combination of these are used, observers do not tend to choose more than two hues to categorize colours and exclude the colour opponent red-green and yellow-blue combinations (Abramov et al., 1992; Boynton et al., 1964). The results show a general agreement in terms of the precise colours of the unique hues, despite minor inter-individual differences (Abramov et al., 1991, 1992; Boynton & Gordon, 1965; Boynton et al., 1964). The hues that are identified with these techniques do not denote exact categories; instead they identify exemplars of typical hues within that category that gradually change into the adjoining one with considerable overlap (**Figure 4.2**).

In this series of experiments we explored the categorization of a colour space using a colour naming paradigm in which observers ranked coloured stimuli into one of four main, often referred to as unique hue categories; red, green, yellow or blue (De Valois et al., 1997b). The coloured stimuli were defined in MBDKL space in which the cardinal axes isolate the activity of the cone opponent mechanisms (Krauskopf et al., 1982). We wished to demonstrate colour naming functions and identify key locations on the resulting colour naming curves such as unique hues, adjacent colour categories and cone opponent mechanisms (**Figure 4.2**). We also looked for individual differences in terms of the locations of these key points. This experiment provided the basis for stimulus choice in the colour memory experiments in **Chapters 4** and **5**.

4.2.2 Methods

A hue naming procedure was performed in preliminary experiments as described by Parry et al. (Parry et al., 2006) in order to obtain a matching

function (p[same]) as a function of the chromatic axis of the stimulus. The experiment involved the scaling of a range of isoluminant colours into the four categories (R, G, B, Y) to form colour naming functions.

Stimuli were defined in CIE xy (1931) colour space based on the 2° standard observer and were also expressed as vectors in the modified MBDKL chromaticity diagram (MacLeod-Boynton chromaticity diagram described by Derrington et al. (Derrington et al., 1984; Krauskopf et al., 1982). The displayed colours were represented in MBDKL colour space (as described in **Chapter 3, Section 3.2.2.2**), in order to make the assessment of the relation between perceptual and opponent processing categories feasible, since this colour space is based on physiological processes and the cardinal axes isolate the activity of the cone opponent mechanisms. In this space hue is defined by the azimuth (ϕ), the angle of its rotation on the isoluminant plane (chromaticity) and luminance is defined by the elevation (Θ), its deviation from the isoluminant plane along the luminance axis (**Figure 4.3**). Modulation within the angle ϕ along the 0°-180° axis is in accordance with the L-M cardinal axis and modulation along the 90°-270° axis is similar to the S-cone cardinal axis as described by Derrington et al. (Derrington et al., 1984). The colours were equally saturated which was defined by the equal length of the vectors so that their endpoints formed a circle around the white point on the isoluminant plane of the MBDKL colour space.

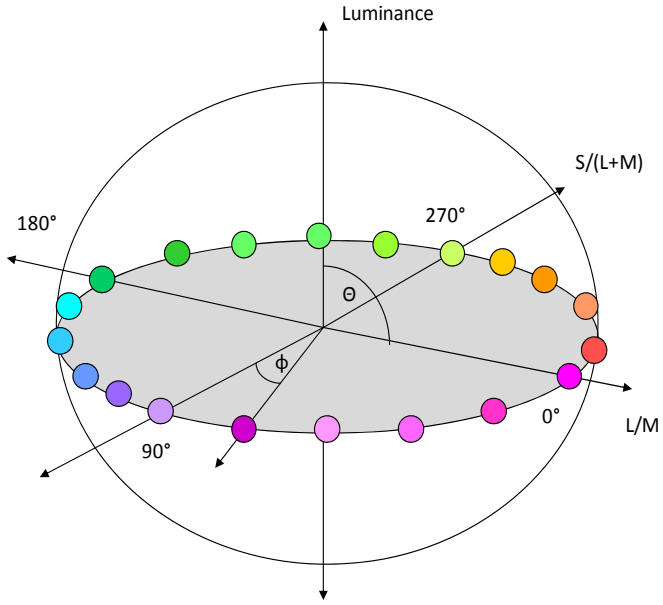


Figure 4.3 The MBDKL colour space and the representative locations of the 20 stimuli that were employed during the hue scaling experiments. The grey area denotes the isoluminant plane. ϕ represents chromaticity and Θ denotes changes in luminance. The capital letters indicate the weighted inputs of the cones into the cone opponent mechanisms. S cone input varies along the 90° - 270° axis, whereas L and M cone excitations vary along the 0° - 180° axis. In case of the intermediary colours that are depicted here there is a combination of the activation of these mechanisms. Modified after Krauskopf et al (Krauskopf et al., 1982).

The stimuli consisted of 20 different coloured patches the chromaticities (saturation, purity) of which were given as equal length vectors in MBDKL colour space that originated from illuminant C. The 20 stimuli had equal saturation and formed a circle on the isoluminant plane (Y = 12.5 cd/m^2) equally spaced around the white point in steps of ϕ = 18° ranging from ϕ = 0° to ϕ = 360° (**Figure 4.3**). Stimulus chromaticities were also expressed as coordinates in the CIE 1931 colour space. These are presented in **Table 3.1 in Chapter 3**. The background was uniform grey of luminance equal to 12.5 cd/m^2, with chromaticity coordinates; x = 0.310, y = 0.316, illuminant C). Stimuli were circular, sharp edged patches the diameter of which subtended 3° of visual angle and were presented on the centre of the monitor for 380 ms.

In a previously described four-alternative forced choice experimental design (De Valois et al., 1997b; Parry et al., 2006) observers were presented with each of the 20 different hues 20 times in a random order and indicated whether the presented colour stimuli appeared blue, green, yellow or red by means of a

response box. The stimuli were displayed for 380 ms and the subsequent stimulus was presented 250 ms after the observer made a response (**Figure 4.4**). There were altogether 400 stimulus presentations and subsequent answers during the course of this experiment. The experiments were performed in a darkened room, usually allowing 10 min for dark adaptation, and 5 min of adaptation to the background illuminant. Observers fixated on a small black fixation mark on the centre of the screen binocularly from a 114 cm viewing distance.

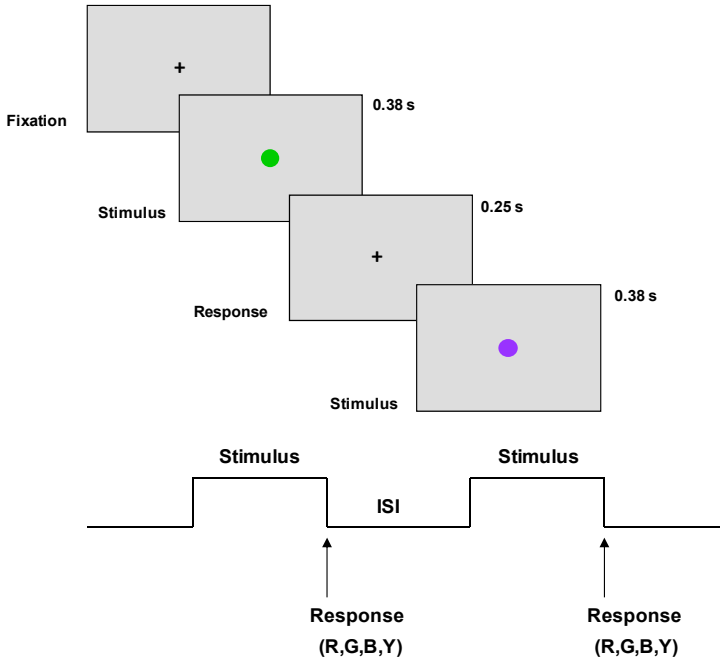


Figure 4.4 Schematic of the colour naming experiment. The observer fixates at the centre of the screen and makes a response after the presentation of the stimulus. The subsequent stimulus appears following the response. Due to randomisation, any of the 20 different hues can appear in the centre of the screen and the available response options are red, green, blue and yellow.

Five observers took part in this experiment (3 females, 2 males; mean age ± 1 SD, 36.2 ± 5.6 years). All had normal colour vision according to Rayleigh matches made on a HMC Anomaloskop (Heidelberg) and the Farnsworth-Munsell 100-Hue test. All had 6/6 or corrected to 6/6 Snellen visual acuity.

The results were analysed by deriving four colour naming functions p[red], p[blue], p[green] and p[yellow], where p[colour] was the proportion of times that a particular test hue was called that colour out of a total of 20 presentations (Parry et al., 2006). 12 colour stimuli for each observer were identified based on

the data (**Figure 4.5**); exemplars of four main hues (red, blue, green and yellow) which were defined as the central maxima of the hue scaling functions, four 'cross-over hues' which corresponded to the axes in colour space where the presented stimuli were equally likely to be identified by adjacent colour appearance mechanisms (R-B, B-G, G-Y and Y-R) and four 'cardinal hues' that corresponded to axes that isolate the activity of the cone opponent mechanisms (ϕ = 0° - 180°, ϕ = 90° - 270°).

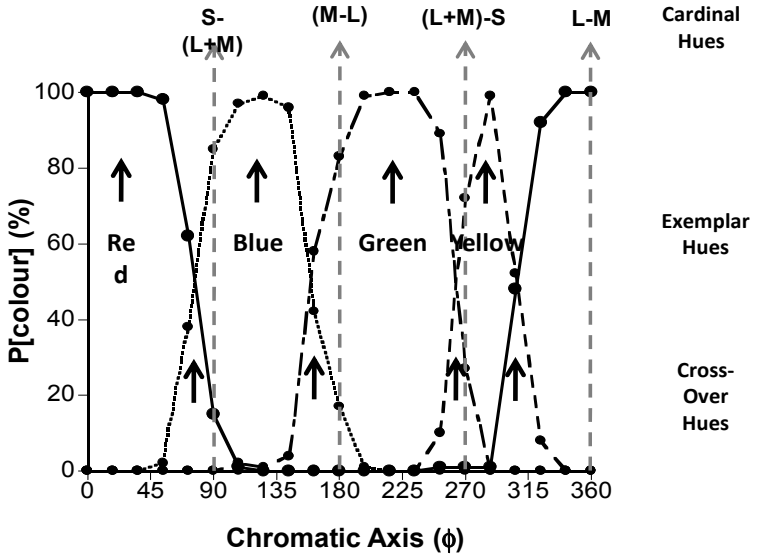


Figure 4.5 Example of hue scaling functions showing the chromatic axes in MBDKL colour space. The hue naming functions are expressed as percentages (p[colour](%)) and plotted as a function of chromatic axis. Dashed grey vertical lines represent the cone opponent mechanisms and the short black arrows point to the perceptual colour categories, namely the Exemplar and the Cross-Over Hues.

4.2.3 Results

In this initial experiment we were interested to know how a colour stimulus is categorized by the individual observer. The matching functions (p[colour]) were plotted as a function of the stimulus chromatic axis, and p[colour] equals to the percentage/fraction of the times the stimuli were reported as being the same hue. The averaged and individual colour naming functions for five of the observers are presented in **Figures 4.6** and **4.7**, respectively. The key points of

the colour naming functions were identified as explained in **Figure 4.5**. Confirming earlier results, the data clearly shows that neither the central maxima nor the crossover points of the colour matching data coincide with the cardinal axes that isolate S, M, L cone activations in the cone opponent mechanisms (De Valois et al., 1997b). Although there is overall agreement in the definition of the basic colour categories, there are some individual differences in terms of the location of the defined unique hues and adjacent colours (**Table 4.1**). This experiment confirms findings from previous studies, namely, that the unique hues do not coincide with the cone opponent mechanisms (De Valois et al., 1997b; Panorgias et al., 2009; Parry et al., 2006).

Table 4.1 Individual and averaged locations of the key chromatic axes expressed as degrees of rotation (ϕ) in MBDKL based on the hue naming functions in case of five observers. The individual values presented here served as reference hues in the experiments presented in **Section 4.3**.

	R	R-B	B	B-G	G	G-Y	Y	Y-R
VN	18	75	117	156	216	261	288	318
AW	0	70	117	165	225	265	288	298
AE	18	68	108	182	225	261	279	306
JH	18	78	108	155	234	280	288	310
DM	18	96	126	156	207	252	279	306
AVG	14.4	77.4	115.2	162.8	221.4	263.8	284.4	307.6
SD	8.049	11.126	7.529	11.476	10.261	10.232	4.929	7.266

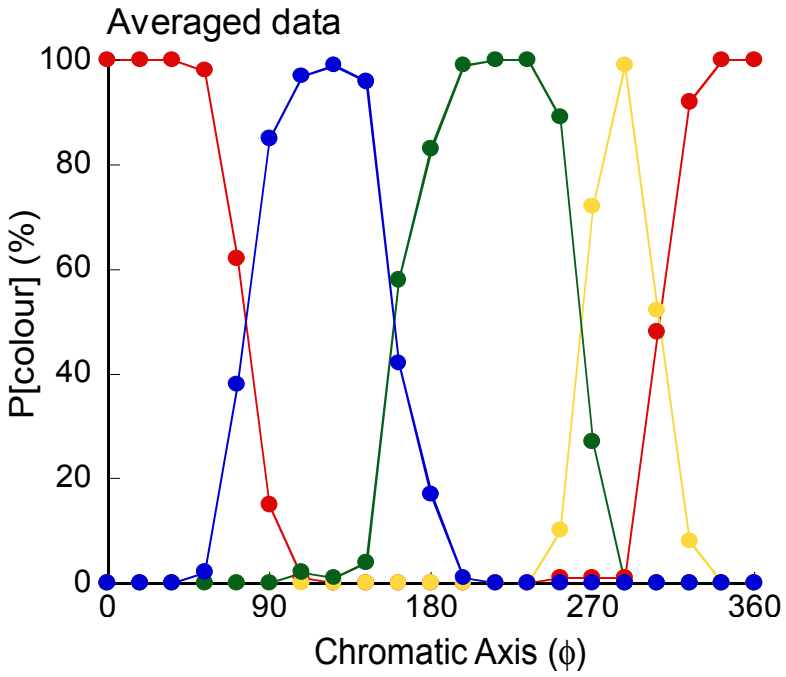


Figure 4.6 Group averaged hue scaling functions (n = 5) showing the chromatic axes in MBDKL colour space. See detailed explanation in text.

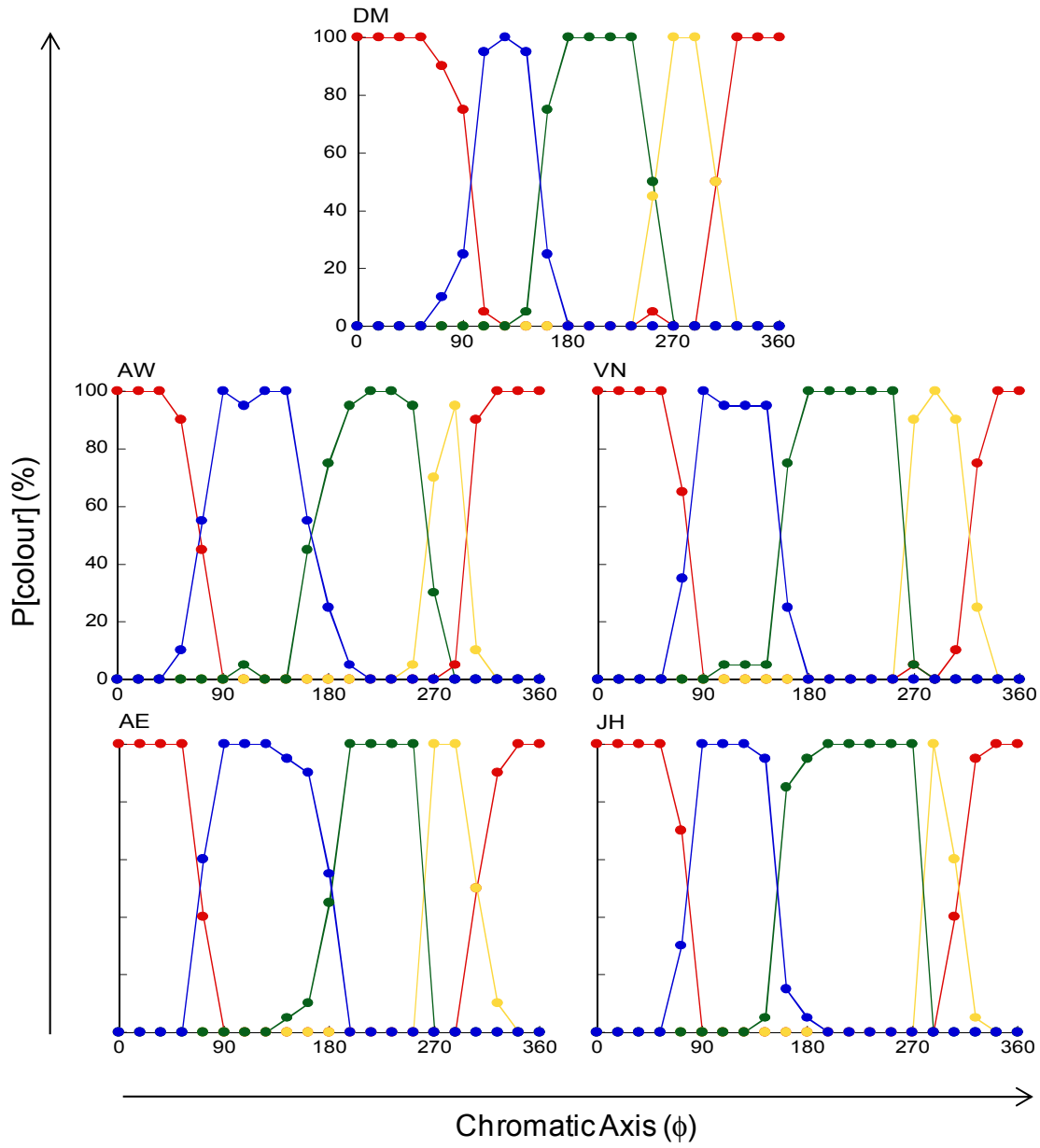


Figure 4.7 Individual data showing the key chromatic axes expressed as degrees of rotation (ϕ) in MBDKL based on the hue naming functions in case of five observers. The individual data show very similar characteristics and locations for the perceptual exemplars of hues which seem to have similar locations for all observers.

4.2.4 Discussion

According to psychophysical and physiological studies, colour processing is well explained by the cone opponent mechanisms from the retina to the level of the LGN, via three post-receptoral processing channels; the magnocellular, parvocellular and koniocellular pathways (Derrington et al., 1984; Krauskopf et al., 1982). Even though electrophysiological experiments identified double

opponent cells in V1 and V2, recent physiological studies showed colour appearance related activity maps in these areas (Conway & Livingstone, 2006; Xiao et al., 2007; Xiao et al., 2003). These cortical areas tend to be more organized around the sensory experience of colours, colours which do not correspond with the neurophysiological properties of the colour opponent cells at sub-cortical levels (**Figure 4.5**). Therefore it is assumed that the processing of colour information undergoes a reorganisation at some point, possibly at cortical level. The exact location where this transformation takes place is still a matter of debate.

Hue names correspond with perceptual colour experience and unique or elementary hues form the four basic colour categories; red, green, yellow and blue and previous experiments have shown that the cone opponent model does not account for the appearance of colour categories (De Valois & De Valois, 1993; Derrington et al., 1984; Gegenfurtner & Kiper, 2003; Lennie et al., 1990). The colour naming functions explored here are similar to the hue scaling results described by DeValois et al. (De Valois et al., 1997a) in the terms that the hues which are defined by the cone opponent mechanisms do not coincide with the perceptually categorized unique hues (**Figures 4.2 and 4.5**).

Even though there are other methods to define unique hues this method is sufficient to locate exemplars of these colour categories, using only one hue term to describe the stimulus. The location of the unique hues that were classified in our experiment are compatible to the ones that were identified in previous experiments (De Valois et al., 1997b; Panorgias et al., 2009; Parry et al., 2006).

In summary, in this initial experiment we have identified exemplars of unique and cross-over hues using a hue naming method. These hues formed the

stimulus set for the subsequent experiments together with the hues that represent the cone opponent mechanisms. The results are in agreement with earlier studies (De Valois et al., 1997b; Parry et al., 2006)

4.3 Colour Memory Experiment

4.3.1 Introduction

The aim of this experiment was to examine VSTM for colour, taking into account the different colour processing mechanisms that are present in the visual system at sub-cortical and cortical levels. As mentioned in the previous section no studies have so far examined differences between VSTM characteristics for colours that are defined by either cone-opponent or colour appearance mechanisms. According to psychophysical experiments there are a number of separate memory mechanisms that are linked with different attributes of visual stimuli and are organised into parallel channels (Magnussen, 2000; Magnussen et al., 1996). In view of the segregated nature of colour processing evident in the sub-cortical and cortical visual pathways, there is a strong possibility that colour constitutes a separate entity from other stimulus dimensions within visual memory. This is an issue which we wish to explore in this chapter. In addition, we also want to investigate the extent to which there might be evidence for the separate storage of different hue categories within sensory memory for colour.

Colour memory has traditionally been described and examined using successive colour matching tasks, where observers matched the stimuli from memory with a previously presented reference stimulus after a time delay has elapsed. These studies have found a minor deterioration in performance which is often expressed as a shift from the original colour. These studies have

produced various results regarding the accuracy of these memory processes, as expressed by hue, brightness and saturation shifts (Burnham & Clark, 1955; Collins, 1932; Hamwi & Landis, 1955; Heider, 1972; Loftus, 1977; Newhall et al., 1957; Nilsson & Nelson, 1981; Perez-Carpinell et al., 1998; Sachtler & Zaidi, 1992). They appear to be inconsistent in terms of their findings, possibly due to a lack of consistent methodological framework across the studies (a more detailed review of this topic can be found in **Chapter 2, Section 2.6.2**).

In the present experiment we wanted to re-examine these issues in view of the current knowledge about the perceptual organisation of colour processing from cone-opponent to perceptual colour mechanisms using a novel approach. The aim was to investigate memory performance for exemplars of unique hues, adjacent hue categories (cross-over hues) and cone opponent (cardinal) mechanisms. Differences between these mechanisms, or correlations between any of these mechanisms and VSTM would provide further information about the organisation of colour information in the visual system. Our hypothesis proposed that VSTM for colour is based on perceptual colour processing, and that such a relationship would result in a higher accuracy for certain colours in memory compared to others i.e. exemplar or unique hues would be retained more accurately than either intermediate or cardinal hues. In order to examine this hypothesis the time course of short term colour memory was assessed for ISIs of up to 10 s. Changes in accuracy, discrimination threshold and hue shifts were examined.

4.3.2 Methods

The stimulus display and configuration were described in detail in the General Methods section (see **Chapter 3, Sections 3.2** and **3.6.1.2**). In this experiment

12 hues were employed as reference stimuli, eight that were previously identified in the hue scaling experiment (**Table 4.1**) and the four hues that represented the cardinal axes of the cone opponent mechanisms (**Figure 4.5**). The chromaticities of the test stimuli were alterations within a predefined range of ϕ = -20° and +20° relative to the reference colour by moving through the colour space in both directions from the reference hue in steps of ϕ = 3° or 4°, for 11 test stimuli for each reference colour. **Figure 4.8a** shows an illustration of an 18° reference and corresponding test stimuli. As can be seen in **Figure 4.8a**, the two extreme colours of this range were easily discriminated from the reference, whereas the hues within the range represented a range of similar colours. The stimuli were circular patches, had sharp edges, their diameter subtended 1.5° of visual angle.

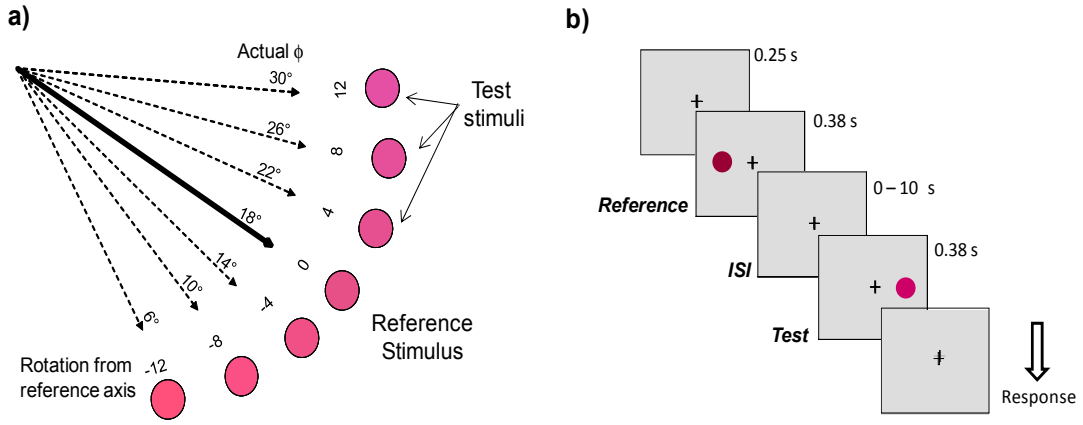


Figure 4.8 Stimulus design and paradigm. The same figure has been presented in **Chapter 3**. Part a) shows illlustration of an exemplar reference axis (ϕ = 18°) and corresponding test stimuli for rotations between ϕ = -12° and +12°. Figure b) illustrates a delayed match-to-sample paradigm. During the experiments, the observer fixates at the centre of the screen, the reference stimulus appears on the left of the fixation mark for 380 ms and after a 0, 1, 5 or 10 s long ISI one of the test stimuli appears on the right of the fixation mark for 380 ms and observers compare the test with the retained hue of the reference making a same versus different judgment.

In a delayed match-to-sample paradigm the reference and test stimuli were presented simultaneously and successively with 1 s, 5 s and 10 s ISI in the different runs. In each run, four of the reference stimuli and their corresponding

test stimulus range were selected (**Figure 4.8b**). The reference stimulus was presented 1.5° away from the central fixation point on the right side, along a horizontal plane and the test stimuli were presented on the left side at the same distance along the horizontal plane (**Figure 4.8**). Each stimulus was presented for 380 ms and the consequent reference stimulus appeared 250 ms after the observer made a response. Typically, four different reference hues and their corresponding test stimuli were combined in a random order in a multiple probe design. Every single reference and test pair was presented ten times. In order to minimise rehearsal effects that would be generated by repeated exposure to the same stimulus, the reference was varied from trial to trial so the observer could not predict which stimulus had to be matched on consecutive trials. There were 110 presentations during each run. Each run lasted approximately 30 - 180 min, and every observer completed approximately 20 experimental runs. The observer's task was to indicate with an appropriate button press whether the presented test stimulus was the same or different from the reference.

Five observers took part in this study (3 females, 2 males; mean age ± 1 SD, 36.2 ± 5.6 years). All had normal colour vision according to Rayleigh matches made on a HMC Anomaloskop and the Farnsworth-Munsell 100-Hue test. All had 6/6 or corrected to 6/6 Snellen visual acuity.

The experiments were performed in a darkened room, usually allowing ten min for dark adaptation. Observers fixated on a small black fixation mark in the centre of the screen binocularly from a 114 cm viewing distance.

4.3.2.1 Data Analysis

4.3.2.1.1 Curve fitting

In order to analyse the data we plotted the percentage of correct matches ('same') for each reference hue and for each ISI as a function of rotation away from the reference axis as explained in **Figure 3.23**. The data showed normal distribution as examined by the Kolmogorov-Smirnov test (70% of data were: $p_{AVG} > 0.05$) and were fitted by a Gaussian function as described in **Section 3.7.2.1**. In this study we examined how the accuracy of the match (a: height of the curve's peak), the discrimination threshold (σ: width of the spread) and the hue shifts (μ: position of the peak in relation to the x-axis) changed as a function of ISI. The discrimination threshold provides information about the sensitivity of the match for each colour. Threshold metrics cannot be used as an absolute measure of performance across the whole colour space because of the perceptual non-uniformities of MBDKL colour space. In order to counteract this problem the performance for each colour axis in the delayed discrimination task was compared to the performance for simultaneous colour matching.

To analyse how the elapsed time affected discrimination thresholds the sensitivity values were expressed as memory indices (MI_σ) which are the ratio of the values during delayed and simultaneous discrimination:

$$MI_\sigma = \frac{\sigma_d}{\sigma_0} \tag{4.1}$$

where; MI_σ is the memory index, σ_d is the discrimination threshold value for delayed matching and σ_0 is the discrimination threshold value for simultaneous matching performance. MI_σ values were plotted as a function of ISI for the different hues.

The height of the peak of the curve was calculated from the equation as the *'a'* value and represented the accuracy of the match, namely, how many times out of the ten presentations the observer responded 'the same' to the colours that appeared the same for him/her. Accuracy indices were calculated in alignment with the memory indices to examine the effect of the increasing ISI on the accuracy of the match:

$$AI_{\sigma} = \frac{a_d}{a_0} \tag{4.2}$$

where; AI_{σ} is the accuracy index, a_d is the accuracy value for delayed matching and a_0 is the accuracy value for simultaneous matching performance. AI_{σ} values were plotted as a function of ISI for the different hues.

The hue shift refers to the rotation of chromatic axis in degrees in CIE 1931 colour space needed in order for the reference stimulus to match the test stimulus after the time delay has elapsed. The stimulus hue was modulated by changing the orientation (chromatic axis) of a straight vector from the background (CIE x,y,= 0.31, 0.316, Y = 12.5 cd/m^2). Calculation of the time delay induced shift of these positions in relation to the x axis gives information about the magnitude of perceived hue shift that occurs with increasing time delay between the matched and the actual hue. The average net differences between the peak positions taken at 0 s and 10 s delays were calculated to compare the induced hue shifts for the 12 different hues examined.

Initially, hue shift values were expressed as vector rotations in MBDKL space and to further address the problems that arise from the perceptual non-uniformity of MBDKL colour space and CIE 1931 xy standard chromaticity diagram, the hue shift values in terms of CIE 1931 xy chromaticity coordinates

were first calculated and then converted into distances in the more perceptually uniform CIEL*a*b *space.

4.3.2.1.2 Statistical analysis

Statistical analysis of the data was performed with SPSS 15.0 (LEAD Technology). Repeated measures 3-way ANOVA was performed on the memory index (MI_{σ}) data to examine:

1) the effect of ISI (2 levels: 0 s and 10 s),

2) differences between the groups of colour stimuli (3 levels: cardinal, exemplar and cross-over hues),

3) differences between individual colour stimuli within the above colour groups (4 levels per group).

Repeated measures 3-way ANOVA was performed on the accuracy index (AI_{σ}) data to examine:

1) the effect of ISI (2 levels: 0 s and 10 s),

2) differences between the groups of colour stimuli (3 levels: cardinal, exemplar and cross-over hues),

3) differences between individual colour stimuli within the above colour groups (4 levels per group).

Repeated measures 2-way ANOVA was conducted on the time induced hue shift values expressed in the three colour spaces (MBDKL, CIE 1931 and CIEL*a*b *) to examine the following effects:

1) differences between the groups of colour stimuli (3 levels: cardinal, exemplar and cross-over hues),

2) differences between individual colour stimuli within the above mentioned colour groups (4 levels per group).

Homogeneity of the variance was examined using Mauchly's test of sphericity and could be assumed for all of the groups. Significance level was set at $p < 0.05$.

4.3.2.1.3 CIE conversion

The equations used for the following calculations are given in **Section 3.2.2.4**. The hue shifts, expressed as vector rotations in MBDKL colour space were calculated for the 10 s delay the following way; the rotation difference between the simultaneous and the 10 s delayed matching was first determined. For the 'between colour space' conversions the ϕ value in case of 0 s and 10 s were converted into CIE(1931) xy coordinates with simple trigonometry, and Euclidean distances between the two coordinates (i.e. position of matched hues in case of 0 s and 10 s delays) were calculated. XYZ tristimulus values were calculated from the CIE 1931 xy coordinates and in the following step, CIEL*a*b* coordinates were calculated from the XYZ tristimulus values. Euclidean distances between the two coordinates (position of matched hues in case of 0 s and 10 s delays) were determined as in case of the CIE 1931 xy colour space. The resulting distances were averaged across observers and were compared for the different colour spaces.

4.3.3 Results

The effects of time delay on accuracy, sensitivity of the match as well as hue shifts were examined. Initially the matching data was fitted with Gaussian curves and **Table 4.3** shows the accuracy of the fits. Goodness of the fit

showed a continuous decrease with increasing ISIs, but R values were above 0.85 in all cases which indicated a good curve fit to the data (**Table 4.3**).

Table 4.3 Mean R values and standard deviations of the Gaussian fits to the colour matching data for the different time delays. The data represents the average across the five observers.

	0 s	1 s	5 s	10 s
R_{AVG}	0.969483	0.91005	0.902433	0.8652
SD	0.009223	0.05208	0.058032	0.102267

4.3.3.1 Memory Index

Figure 4.9 shows the averaged MI_{σ} values for the five observers as a function of ISI for the cardinal, exemplar and cross-over hues. Error bars indicate ± 1 S.D. In these plots an index of 1 indicates that colour matching performance remains unchanged with increasing ISI compared to the simultaneous matching condition. Values greater than 1 are indicative of deterioration in performance and, as can be observed in **Figure 4.9**, for each of the 12 chromatic stimuli tested there is a consistent increase in the memory index values as a function of ISI. The error bars indicate that data is highly variable, but overall the pattern that emerges is consistent.

A repeated measures 3-way ANOVA showed a main effect of ISI on memory index values ($F_{1,4}$ = 174.67; $p < 0.001$) for all stimuli, but there was no statistically significant difference in performance between any of the colour groups ($F_{2,8}$ = 1.43; $p = 0.294$), nor between any of the individual chromatic stimuli ($F_{3,12}$ = 0.749; $p = 0.544$).

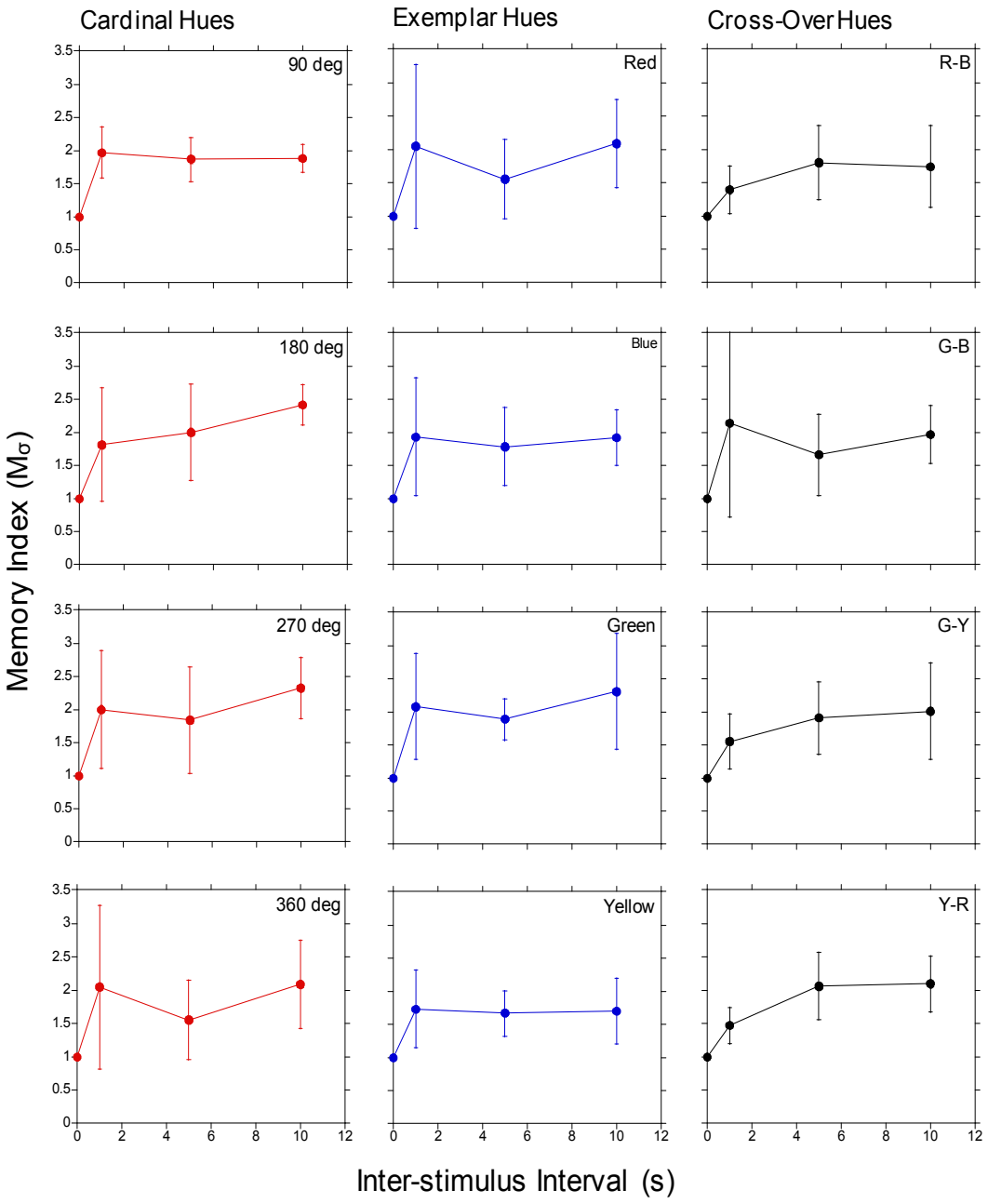


Figure 4.9 Memory index (MI_σ) values for the key chromatic stimuli. The figures show the group averaged data for the five observers plotted as a function of time delay. The three different categories of stimuli (cardinal, exemplar and cross-over hues) are depicted on separated graphs. The error bars represent ± SD. (R-B: red-blue, B-G: blue-green, G-Y: green-yellow, Y-R: yellow-red).

4.3.3.2 Accuracy Index

Figure 4.10 shows the averaged AI_a values for the five observers, as a function of ISI for the cardinal, exemplar and cross-over hues. Error bars indicate ±1 SD. In these plots an index of 1 indicates that colour matching performance remains unchanged with increasing ISI, compared to the simultaneous matching

condition. Values smaller than 1 are indicative of deterioration in the accuracy of the match and, as can be observed in **Figure 4.10**, for each of the 12 chromatic stimuli tested there is a minor but consistent decrease in the accuracy index values as a function of ISI. The error bars indicate that the data is variable but overall the pattern that emerges is consistent. Since the accuracy values represent how many times out of the ten presentations the observer responded 'the same' to the colours that appeared the same for her/him it can be concluded that as the time delay is introduced the retention of the colour in VSTM becomes less accurate.

However, a repeated measures 3-way ANOVA showed no main effect of ISI on accuracy index values ($F_{1,4}$ = 6.488; p = 0.063) and there was no statistically significant difference in performance between any of the colour groups ($F_{2,8}$ = 0.602; p = 0.571), nor between any of the individual chromatic stimuli ($F_{3,12}$ = 3.288; p = 0.058).

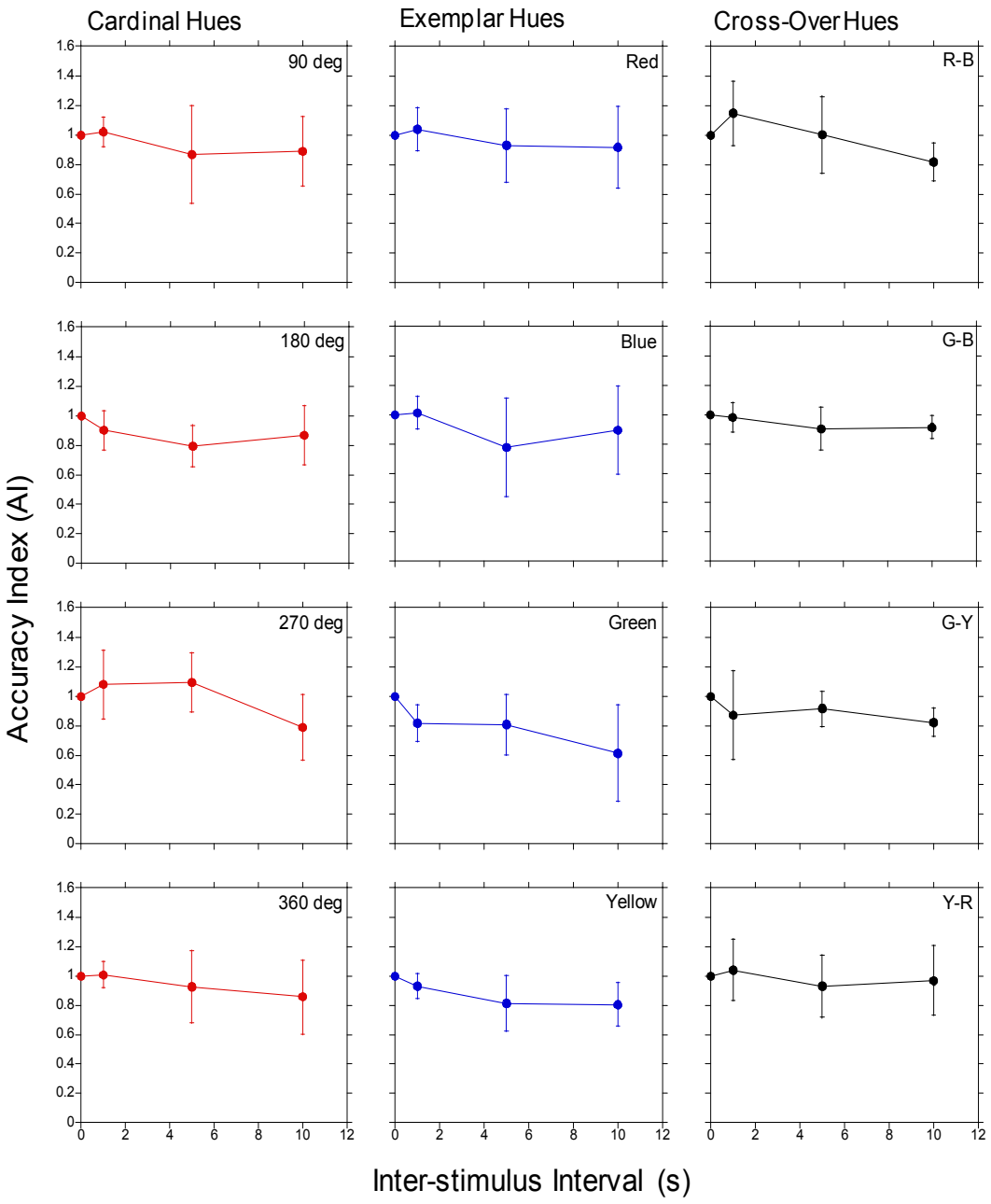


Figure 4.10 Accuracy Index values for the key chromatic stimuli. The figures show the group averaged data for the five observers plotted as a function of time delay. The three different categories of stimuli (cardinal, exemplar and cross-over hues) are depicted on separated graphs. The error bars represent ± 1 SD. (R-B: red-blue, B-G: blue-green, G-Y: green-yellow, Y-R: yellow-red).

4.3.3.3 Hue Shifts

Figure 4.11 shows the hue shift values as a function of ISI. It is apparent from the data that the different hues show a gradually increasing degree of perceived shift in memory to different directions with increasing time delays, and in case of most hues this initial direction remains consistent. **Figure 4.12a** shows the hue

shift values in MBDKL colour space indicating the degree of the vector rotation that was needed to make a test stimulus match the reference stimulus. The large error bars indicate that even though the trend that emerges here is consistent, the data is highly variable (**Figure 4.11** and **4.12**). **Figure 4.12** shows the group averaged differences in matched hues for the reference and test stimuli when they were presented simultaneously (ISI = 0 s) compared to the longest delay (ISI = 10 s) expressed in three different colour spaces. The magnitudes of these hue shifts are shown for all stimuli in order to qualitatively demonstrate how the perceived stimulus hues were affected by the introduction of memory delay. **Figure 4.12b** and **c** represent the hue shifts in terms of the distances between the actual and matched stimulus co-ordinates in CIE 1931 xy and CIEL*a*b* colour space, respectively. The magnitude of the hue shifts is different in cases of the different colours; some chromatic axes undergo larger shifts than others and some require little or no rotation in order to generate a match. A repeated measures 2-way ANOVA showed a significant main effect of colour group in all three colour spaces (CIE 1931: $F_{2,8} = 5.59$, $p = 0.030$; CIEL*a*b*: $F_{2,8} = 4.85$, $p = 0.042$; MBDKL: $F_{2,8} = 5.60$, $p = 0.030$). **Figure 4.12** shows that this main effect is due to the higher mean for the cardinal group compared to the exemplar and cross-over groups. There was no significant difference between individual colours within the groups ($p > 0.528$ for all three colour spaces). Exemplar hues appear to undergo the smallest hue shifts as a function of ISI.

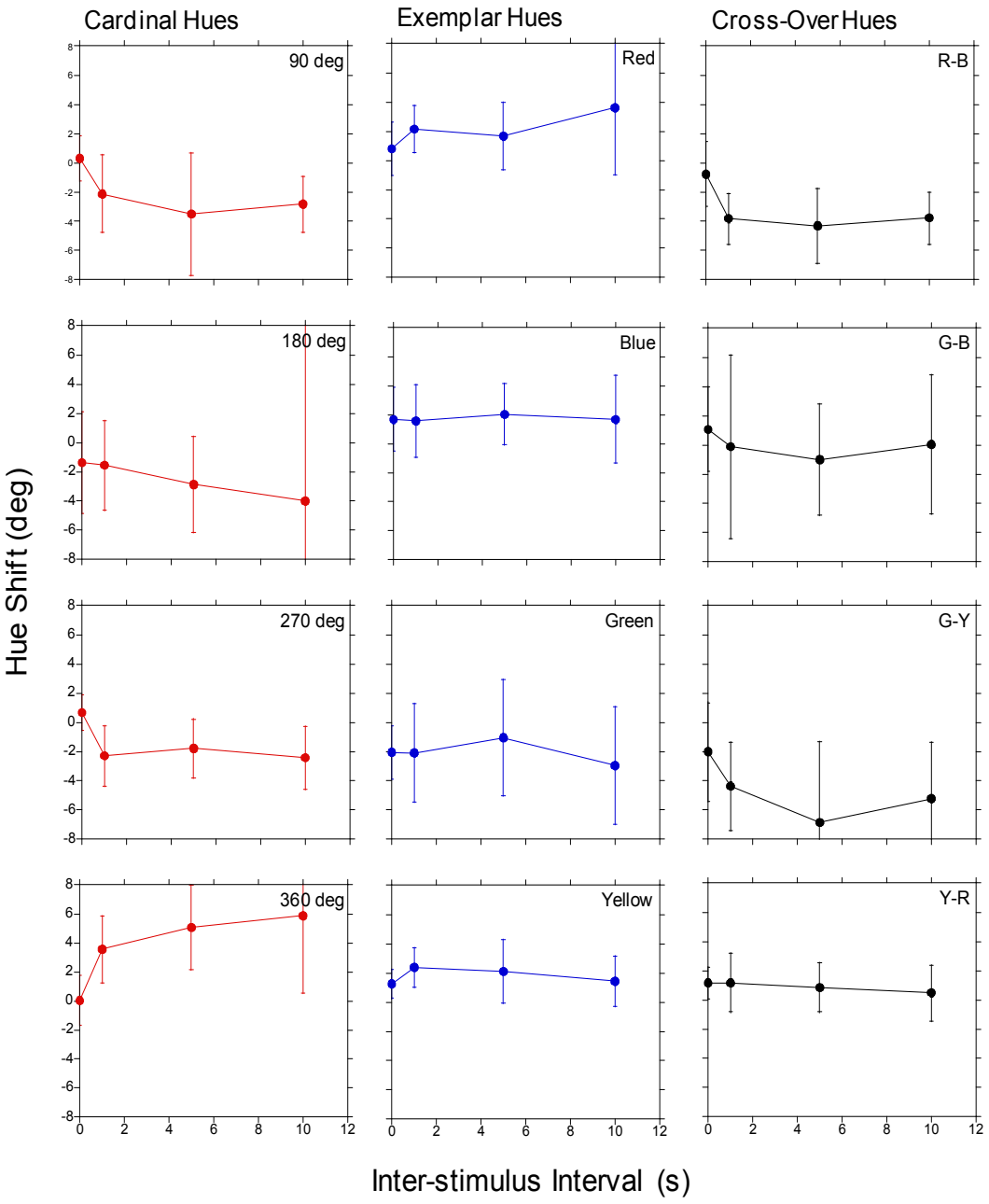


Figure 4.11 Hue shift (vector rotation in degrees) values for the examined key chromatic axes. The figures show the group averaged data for the five observers plotted as a function of time delay. As before, the three different categories of colours (cardinal, exemplar and cross-over hues) are depicted on separated graphs. The intercept points of the curves indicate the positions of the peak in the simultaneous matching condition. The error bars represent ±1 SD. (R-B: red-blue, B-G: blue-green, G-Y: green-yellow, Y-R: yellow-red).

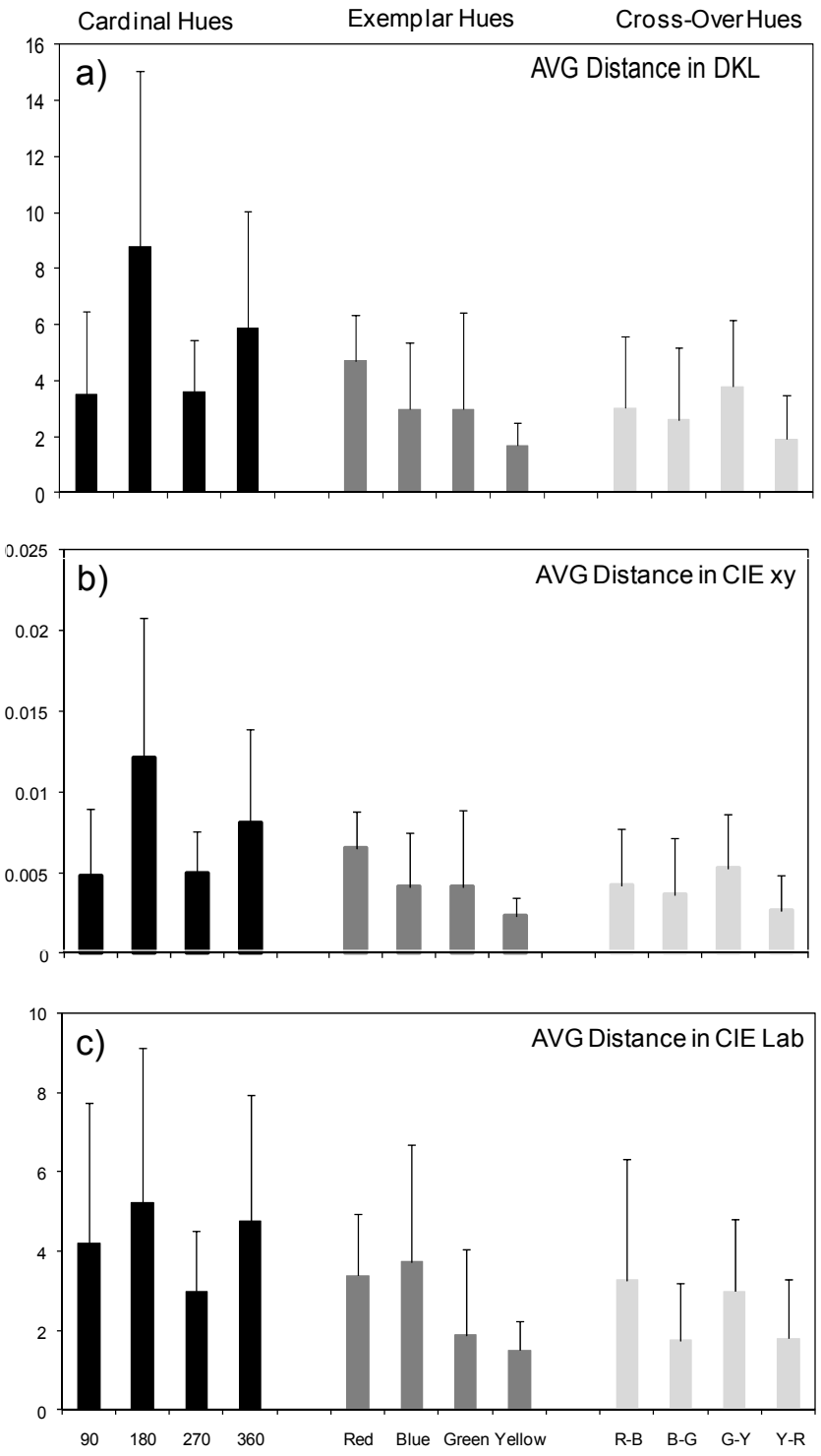


Figure 4.12 Bar plots for all observers showing averaged Hue shift values for the examined colour categories (cardinal, exemplar and cross-over hues). Error bars indicate ±1 SD. The figures show the group averaged hue shifts between the matches made for the 10 s and 0 s ISIs in a) MBDKL, b) CIE1931 (x, y, z) and c) CIE (L*a*b*) colour spaces. The error bars represent ±1 SD.

4.3.4 Discussion

Many studies on colour memory have found differences in the accuracy of memory for different hue categories, but without clear consistency regarding which hues are remembered better than others in VSTM. For example, Collins (Collins, 1932) showed that certain green and red wavelengths were more difficult to remember than others. According to Nilsson and Nelson (Nilsson & Nelson, 1981), violets, green-blues and yellow-oranges were remembered better; whilst Jin and Shevell (Jin & Shevell, 1996) proposed that long and medium wavelength colours were retained better in memory compared to short wavelength colours.

In this experiment, the extent to which information about stimulus colour can be retained by VSTM over short time delays of up to 10 s was examined using a delayed matching task. The decrease in the ability of human observers to discriminate successively presented coloured stimuli, as the temporal separation between them increases, was measured. Consistent with previous work, decay in visual short term memory over time was found (Hamwi & Landis, 1955; Newhall et al., 1957; Nilsson & Nelson, 1981; Perez-Carpinell et al., 1998). Moreover, the results presented here suggest that the decay in discriminative ability over time is similar for all of the coloured stimuli that were tested.

Differences between coloured stimuli, in terms of the extent to which their remembered hues shifted away from their actual hues over time delays (ISIs), have also been examined. It was of particular interest in this study to examine whether there were any differences between stimuli that isolated the activity of cone-opponent (cardinal) mechanisms as opposed to those which were related to colour appearance mechanisms. Crucially, the colours that represent red,

green, yellow and blue colour categories do not correspond to the cone-opponent axes, or indeed any aspect of physiological organisation that exists for colour processing in the pre-cortical visual pathway (De Valois et al., 1997a). Whilst there may be little correlation between colour appearance mechanisms and pre-cortical colour processing, it was of particular interest as to whether the former or the latter might provide a basis upon which colour sensory information is organised in 'higher' cognitive functions such as short term memory. These experiments have shown that for the longest ISI (10 s) the shifts in hue between the matched and the reference stimuli are significantly greater for the cardinal stimuli compared to either the exemplar or cross-over hues which were defined in the preliminary scaling experiments. This result raises the possibility that the retention of hues in VSTM that are related to perceptual colour categories are more resistant to deterioration over time than those which isolate pre-cortical processing mechanisms. Similar findings have been previously reported for focal colours which are more accurately remembered than non-focal colours (Boynton & Olson, 1990; Heider, 1972).

The importance of colour appearance mechanisms in short term colour memory points to the fact that colours are unlikely to be memorized solely on a sensory basis. The fact that perceptually relevant colour categories appear to be more resistant to shifts in their hue as a function of ISI may be indicative of an enhanced ability to apply a verbal tag to a particular stimulus that may help in the retention of colour information (Davidoff & Ostergaard, 1984). Whilst colour itself may be memorised on the basis of sensory information, work has shown that this may be strongly influenced by verbal coding (Bornstein et al., 1976), which neuroimaging studies suggest may involve very different cortical networks (Ikeda & Osaka, 2007). Other more long term mechanisms are also

likely to be involved in how information about colour is retained in memory. Many objects that are encountered in everyday life have a typical colour that is closely associated with them, termed a memory colour. For example, when thinking of a banana or a strawberry one may have in mind a particular yellow or red colour, respectively. Hansen et al. (Hansen et al., 2007) have shown that these long term memory colours can actually influence and distort incoming colour sensory information. Therefore, the accuracy of information about colour that is retained in VSTM is likely to be the result of interactions between basic low-level, bottom-up sensory input which is subject to modification by more top-down, higher level cognitive processes.

One of the weaknesses of studies that employ perceptually non-uniform colour spaces such as MBDKL is that distances at various locations in the space do not correspond to equal perceptual differences. However, by converting the hue shift values into differences in the perceptually uniform CIE Lu'v' colour space we showed that our deductions were not affected by the limitations of MBDKL or CIE 1931 xy colour spaces.

The fundamental finding of this experiment is that as coloured stimuli are analysed with increasing time delay, the perceived hue shifts are not uniform across colour space; there seem to be hues that are invariant, namely, the unique hues. Some other hues undergo larger shifts and show greater variation, and those hues tend to be coincident with the cardinal axes and adjoining colour categories, probably because they are less defined in terms of colour appearance mechanisms.

The hues that undergo minimum shifts are not coincident with the cone opponent mechanisms, and suggest they do have a special status in VSTM. This study has found that the representation of unique hues seems to be more

stable in memory, which is reflected on the significantly smaller hue shifts. This might denote that there is a link between short term memory for colour and colour appearance mechanisms (i.e. higher order colour perception), which might form the basis of colour information storage in short term memory.

In conclusion, we have found a decay in performance in VSTM for hues which was worse in case of the cardinal hues as compared to the exemplar and cross-over hues. This difference in performance was indicated by greater hue shifts after a 10 s in a delayed matching task and might indicate that perceptual hue mechanisms serve the basis on which colour information is organised in VSTM. These results were not affected by the perceptual nonuniformity of MBDKL or CIE 1931 xy colour spaces. Accuracy of the match and discrimination ability were also examined and indicated no significant changes as a function of time delay or colour group.

Chapter 5

The Retention and Disruption of Colour Information in Visual Short Term Memory – Colour Memory Masking

5.1 Introduction

There is increasing evidence that the mechanisms that take part in the short term storage of elemental visual information are closely linked with the ones that perform their sensory analysis (Magnussen, 2000; Pasternak & Greenlee, 2005). These systems work together as a network that has a dual function involving the sensory encoding and short term storage of the information. The short term storage of visual information has been studied at both behavioural and single neuronal levels (Bisley et al., 2004; Magnussen & Greenlee, 1992; Magnussen et al., 1996). These studies have indicated the existence of parallel, high fidelity mechanisms linked to memory formation, which are dedicated to specific aspects of a visual stimulus, such as orientation, spatial frequency, velocity and contrast (Greenlee et al., 1991a; Greenlee et al., 1995; Magnussen, 2000; Magnussen & Greenlee, 1985, 1992; Magnussen et al., 1991; Nilsson & Nelson, 1981). VSTM has traditionally been examined using delayed discrimination tasks during which two stimuli; reference and test have

been typically presented with ISIs of between 1 - 30 s. The task for the observer is to decide whether the reference and test have the same or different properties with regards to a particular stimulus dimension. In these experiments, the effect of the time delay on the ability of the observer to perform the task is expressed by a discrimination threshold or changes in the point of subjective equality (PSE). The discrimination thresholds show a high degree of accuracy in working memory for most of the stimulus dimensions. Information appears to be retained in memory with relatively little loss for up to 30 s (Magnussen & Greenlee, 1999; Magnussen et al., 2003).

Studies have demonstrated that the retention of information in visual short term memory (VSTM) for basic visual attributes, such as motion, can be disrupted by the presentation of masking stimuli during inter-stimulus intervals (ISIs). These effects are outside the range of traditional sensory masking (Magnussen & Greenlee, 1992). A key finding for 'memory masking' is that it only occurs when the mask and reference stimuli differ in terms of the examined stimulus dimension, for example, spatial frequency discrimination is not affected by a mask that has a different orientation. The selective nature of these memory masking effects suggests a modular organization for VSTM, namely, that it contains parallel stores each tuned to a relatively narrow range of stimulus parameters that are closely linked to visual discrimination mechanisms (Magnussen, 2000).

According to Clifford et al. (Clifford et al., 2003), the majority of neurons in the LGN and V1 receive linear cone inputs and as a result show broad chromatic tuning with a bandwidth of approximately 60° (i.e. cosine chromatic tuning) (De Valois et al., 2000a; Derrington et al., 1984; Lennie et al., 1990). However,

according to Goda and Fuji (Goda & Fujii, 2001), who examined colour discrimination ability of different coloured patterns, the channels responsible for carrying out this task are more narrowly tuned (approximately 40°). Clifford et al. found a bandwidth of 25.1° in a chromatic tilt illusion experiment (Clifford et al., 2003), which is in accordance with the bandwidths found in another experiment that examined chromatic tuning in higher cortical areas such as V2 (Kiper et al., 1997). This implies that cortical mechanisms for the sensory processing of colour information are more narrowly tuned than sub-cortical ones as a result of nonlinear combination of cone signals.

Previous studies have shown that the accuracy of colour information decreases in memory which manifests in hue, brightness and saturation shifts from the originally remembered colour as well as increased discrimination thresholds (Bartleson, 1960; Burnham & Clark, 1954; Burnham & Clark, 1955; Collins, 1932; Jin & Shevell, 1996; Newhall et al., 1957; Nilsson & Nelson, 1981) (further details on this topic can be found in **Chapter 2, Section 2.6.2**).

In this chapter we aimed to explore the basis on which colour might be organized in VSTM, whether it constitutes a separate entity and whether there are parallel mechanisms for different colour categories in VSTM, similar to those which that been shown for other stimulus dimensions such as spatial frequency and speed (Magnussen, 2000; Magnussen & Greenlee, 1992). One way to investigate the organisation of visual information in short term memory is by means of a 'memory masking' paradigm. In this study we employed a colour memory mask to determine whether VSTM displays selectivity for stimulus colour, saturation and luminance content. We expected to find evidence for the idea that colour represents a distinct mechanism in VSTM. We have previously

shown that unique hues have a special status in VSTM (**Chapter 4**) and we hypothesised if VSTM for colour is based upon higher order colour appearance mechanisms such as unique hues, such experiments might reveal four parallel storage mechanisms with relatively narrow bandwidths as compared to the sub-cortical colour processing mechanisms (Boynton & Olson, 1990; Clifford et al., 2003).

5.2 Colour Selectivity of Memory Masking

5.2.1 Introduction

In addition to the spatial and temporal aspects of a visual scene, another important dimension is its colour composition, from which the visual system can extract information about the surrounding environment. The sensory analysis of colour is based upon anatomically segregated and physiologically distinct processing pathways (Gegenfurtner & Kiper, 2003; Solomon & Lennie, 2007). Sub-cortical colour processing is based upon outputs from L-(long), M-(middle) and S-(short) wavelength sensitive cones, which interact in a linear manner to form 'red-green' (L-M) and 'blue-yellow' (S-(L+M)) opponent mechanisms. This cone-opponent model has explained several psychophysical and electrophysiological observations in colour vision (De Valois et al., 1966a; Derrington et al., 1984; Mullen & Losada, 1994). However, within the visual cortex the neural processing of colour appears to undergo a transformation. Numerous experimental observations, both behavioural and neurophysiological, clearly point to the existence of more than two chromatic mechanisms with spectral sensitivities that are very different from that of the cone-opponent channels (Clifford et al., 2003; Conway, 2003; De Valois et al., 2000a; De Valois

et al., 1997b; Eskew, 2009; Goda & Fujii, 2001; Krauskopf, 1999; Lennie et al., 1990; Li & Lennie, 1997; McGraw et al., 2004; Webster & Mollon, 1991; Xiao et al., 2007; Zaidi & Halevy, 1993). Moreover, these so-called 'higher-order' chromatic mechanisms have been shown to have narrow spectral tuning (approx. 35° - 45°) (Goda & Fujii, 2001), a property which can only arise as a result of non-linear combinations of cone inputs (De Valois et al., 2000a; De Valois & De Valois, 1993; De Valois et al., 2000b). This property further differentiates them from cone-opponent mechanisms that are based upon linear combinations of cone inputs and have a more spectrally broadband tuning with a bandwidth of around 60° in the cardinal directions (De Valois et al., 2000a; De Valois & De Valois, 1993; Derrington et al., 1984; Goda & Fujii, 2001; Lennie et al., 1990).

The aim of these experiments was to examine the extent to which perceptual memory displays selectivity for stimulus colour. We used the memory masking paradigm in order to assess how the chromaticity of a masking stimulus determines the extent to which it can interfere with the fidelity of a stored representation of a coloured stimulus. This paradigm has been successful in previous experiments in revealing the spatial tuning and speed selectivity of perceptual memory (Magnussen & Greenlee, 1992; Magnussen et al., 1991; McKeefry et al., 2007). We first aimed to explore whether there are parallel stores for stimulus colour in VSTM. If this is indeed the case, then we aim to examine on what basis colour is organised in short term perceptual memory. If memory masking experiments do reveal some form of colour selectivity, then another question to explore is whether this organisation reflects a linear, broadband cone-opponent processing mechanism that predominates in sub-cortical and early cortical pathways, or instead is the result of contributions from

non-linear, narrowband higher order colour processing. By examining VSTM for colour both from the point of view of cone-opponent and higher order colour processing we take the novel approach of trying to link the sensory analysis of colour information and its retention in perceptual memory (Pasternak & Greenlee, 2005).

5.2.2 Methods

The colour stimuli used in these experiments consisted of hard edged circular coloured patches that subtended 1.5° and were presented on a uniform grey background of the same mean luminance (12.5 cd/m^2). For a detailed description of the display of the stimulus see **Chapter 3, Section 3.2**.

The chromaticities of the colour stimuli were specified as equal length vectors in MBDKL colour space (Derrington et al., 1984), which were defined by their angle of rotation (ϕ) in the isoluminant plane (**Figure 3.5**). The endpoints of these vectors formed a circle around illuminant C (CIE 1931 chromaticity co-ordinates; x = 0.310, y = 0.316) (see details in **Chapter 3**, **section, 3.2.2.2**).

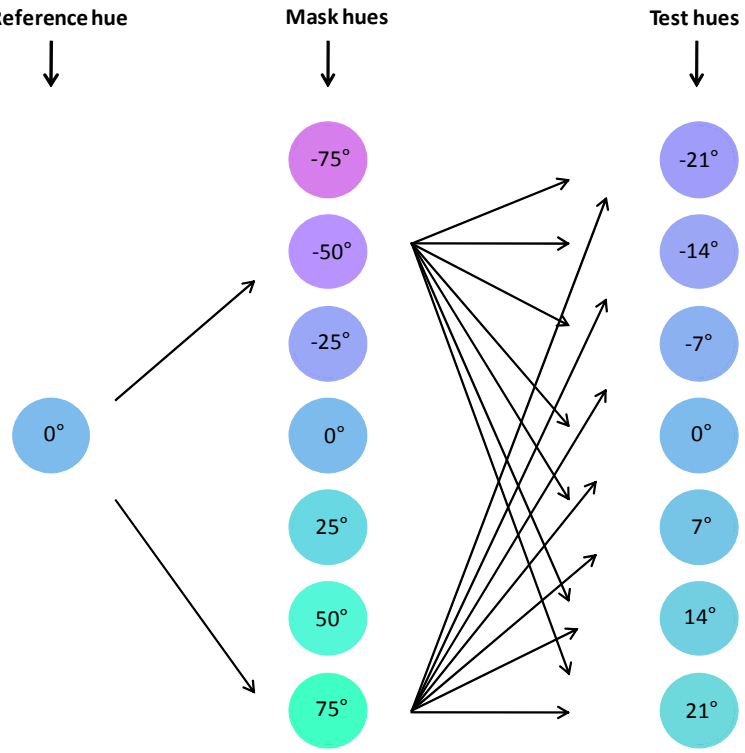


Figure 5.1 Schematic representation of the employed stimulus hues (Exact replica of **Figure 3.19,** for the guidance of the reader). See detailed explanation in text.

Four main reference stimuli were used in this set of experiments, ones which were reported by the individual observers as being exemplars of four main colour categories red, green, blue and yellow. These were determined in preliminary hue naming experiments, which were performed in order to determine their location in MBDKL colour space (See **Chapter 4, section 4.2**).

The test stimulus could be one of seven colours, which sampled equally (in terms of ϕ) a range of hues ($\phi = \pm 21°$) on the isoluminant colour circle either side of the reference stimulus colour (**Figure 5.1**). The range of the test stimuli was determined in preliminary runs so that the two endpoint colours were 100 % discriminable from the reference stimulus. Seven mask hues were taken from a wider range of colours ($\phi_{reference} = \pm 75°$) in steps of 25°.

In an additional experiment, which examined the effect of the mask colour around the whole colour circle, 18 hues in steps of 20° in colour space were chosen as mask stimuli.

A delayed colour discrimination paradigm was used to measure the fidelity of stored colour information in perceptual memory and employed a two-alternative-forced-choice procedure in conjunction with a method of constant stimuli. Each trial began with the presentation of a reference stimulus (red, green, yellow or blue), for a duration of 380 ms, which was followed by a 5 s long ISI. Mask stimuli of variable chromaticity were presented for 2 s in the middle of the ISI in the different runs. At the end of the 5 s ISI the test stimulus (one hue at a time) was presented for 380 ms (**Figure 5.2**). In order to prevent the build-up of long term representations of the stimuli, the reference and test stimuli were presented in a random order. The 'no mask' condition served as a measure of baseline performance against which performance during the mask conditions could be compared (**Figure 5.2**). The reference, mask and test stimuli were separated horizontally to avoid retinal adaptation effects. The reference was presented 1.5° to the right of the fixation point, the mask stimulus was centred on the fixation point and the test was presented 1.5° to the left of fixation (**Figure 5.2**).

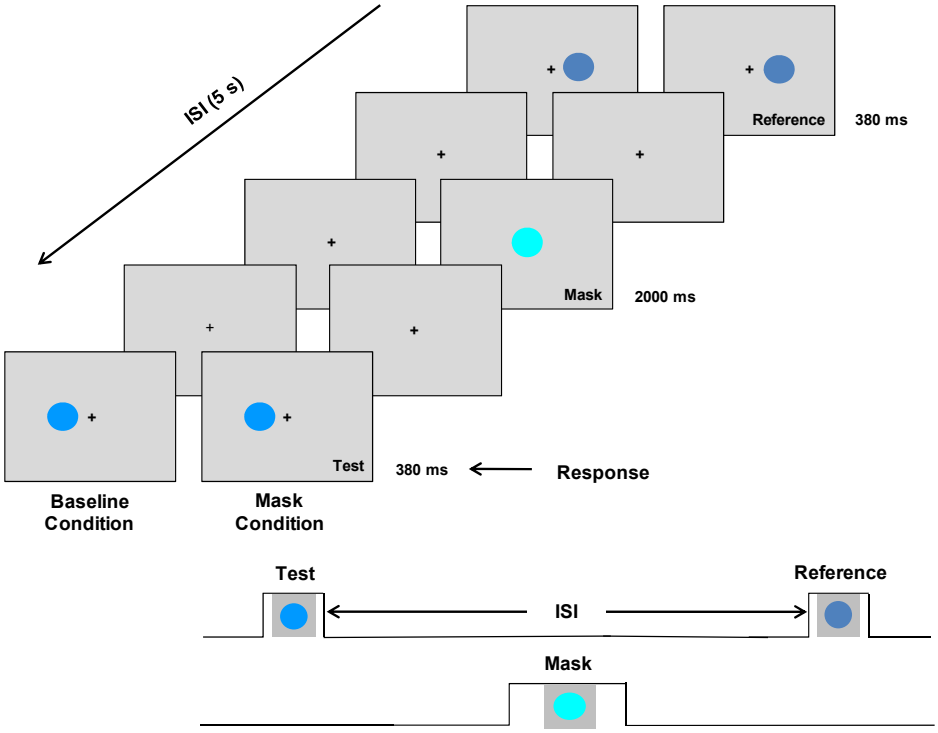


Figure 5.2 Schematic representation of the delayed match to sample paradigm. During the procedure the reference stimulus appeared 1.5° to the right of the fixation mark for 380 ms, which was followed by a 5 s ISI before the test stimulus appeared 1.5° to the left of the fixation mark for 380 ms. After the offset of the test the observers were asked to respond. Without mask condition served as baseline performance, whereas in the masking conditions an additional stimulus appeared before the test hue, on the centre of the screen during the ISI for 2 s.

Following the end of each trial, the observers were instructed to make a response by a button press (CB3 response box; Cambridge Research Systems) to indicate where they considered the test stimulus hue to be located on the colour circle relative to that of the remembered reference colour. In practice, this meant that for a blue reference stimulus, for example, observers were instructed to indicate whether the test stimulus appeared to be more 'green' or 'purple'; in case of a red stimulus the possible responses were whether the test was more 'purple' or 'orange', in case of a yellow reference whether the test was more 'orange' or 'green' and finally, in case of a green reference whether the test was more 'blue' or 'yellow'. This procedure enabled us to plot psychometric functions which allowed us to assess the effects of different mask stimuli on performance, in particular the extent to which mask stimuli affected the point of subjective

equality (PSE) between the test and remembered reference colours. Performance on this delayed colour discrimination paradigm was assessed relative to performance on the baseline condition, where no mask stimulus was introduced during the ISI.

Five observers took part in the study (3 females and 2 males; mean age = 36.2 years, S.D. = ±5.6 years), two of whom were experienced observers and the remaining three were naive as to the aims of the experiment. All gave informed consent and had normal colour vision according to Rayleigh matches made on a HMC Anomaloskop and the Farnsworth-Munsell 100-Hue test. All had 6/6 or corrected to 6/6 Snellen visual acuity. The experiments were performed in a darkened room and observers fixated on a small black cross on the centre of the screen which was viewed binocularly from a distance of 114 cm.

The behavioural data were fitted by a logistic function as explained in detail in **Section 3.7.2.2**. The resulting PSE data were plotted as a function of mask chromatic axis and fitted by a first derivative of a Gaussian function as described in detail in **Section 3.7.2.3**.

5.2.3 Results

Figure 5.3 shows representative individual data for the four main reference stimulus colours. For each reference colour, the graphs plot how PSE varies as a function of mask stimulus colour. The PSEs are specified in terms of the rotation of the chromatic axis in MBDKL colour space of the matched test stimulus, relative to the reference. Baseline conditions (i.e. no-mask), indicated by horizontal dashed lines serve as a basis for comparison. Vertical dashed lines highlight the condition where the mask has identical hue to the reference.

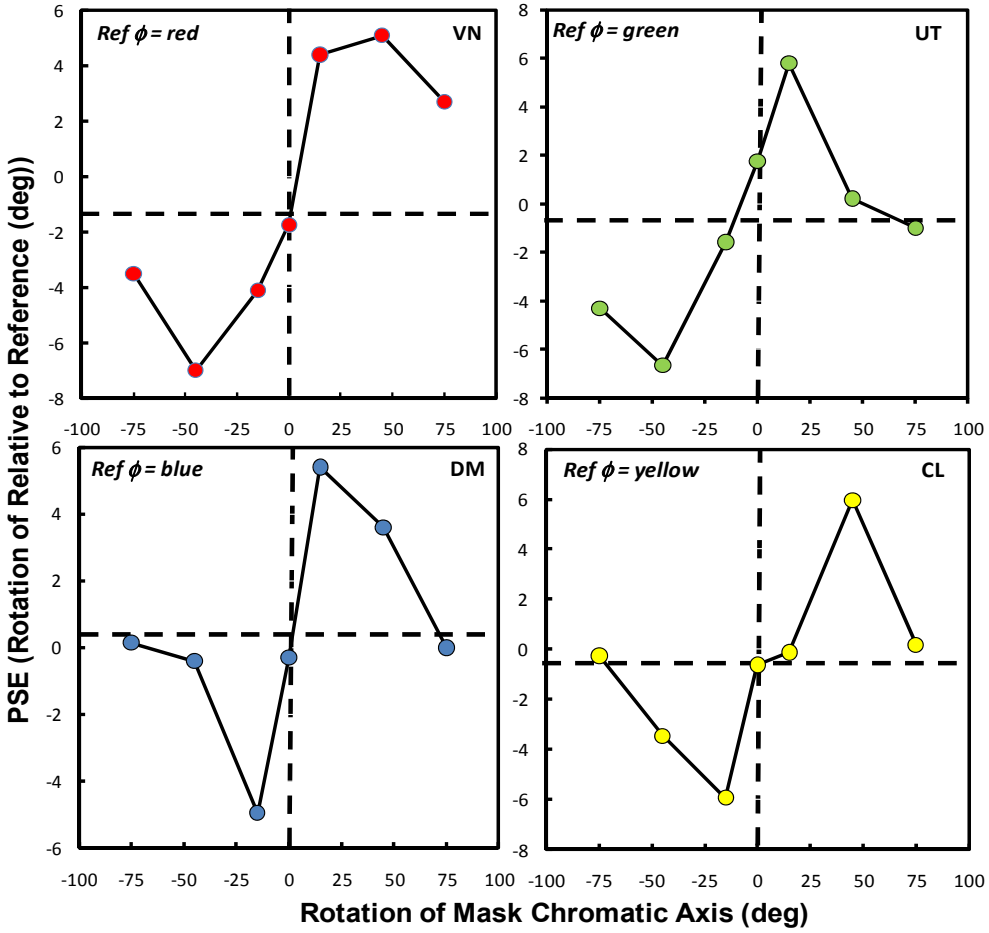


Figure 5.3 Representative single observer data from the colour memory masking experiment. Results in case of the four reference colours are shown for four randomly selected observers. PSE values are plotted as a function of relative rotation of mask chromatic axis. The horizontal dashed lines indicate baseline (i.e. no mask) memory performance and the vertical dashed lines indicate conditions where the reference and the mask stimuli have the same colour.

A consistent trend seemed to emerge on **Figure 5.3**, therefore in the next step we averaged the data from the five observers to observe the effect of the mask (**Figure 5.4**). When the axis of the mask rotates in clockwise direction in colour space (positive relative rotation) the matches made by the observers are 'pulled' in the same direction as the mask, away from the baseline value. The deviation from baseline reaches a maximum with increasing rotation but then starts to decrease and approaches baseline levels as mask chromaticity shifts even further away from the reference. When mask chromatic axis rotates away from the reference in an anti-clockwise direction (negative relative rotations) the

PSEs are shifted in the opposite direction in a similar fashion, reaching a maximum and then returning to baseline.

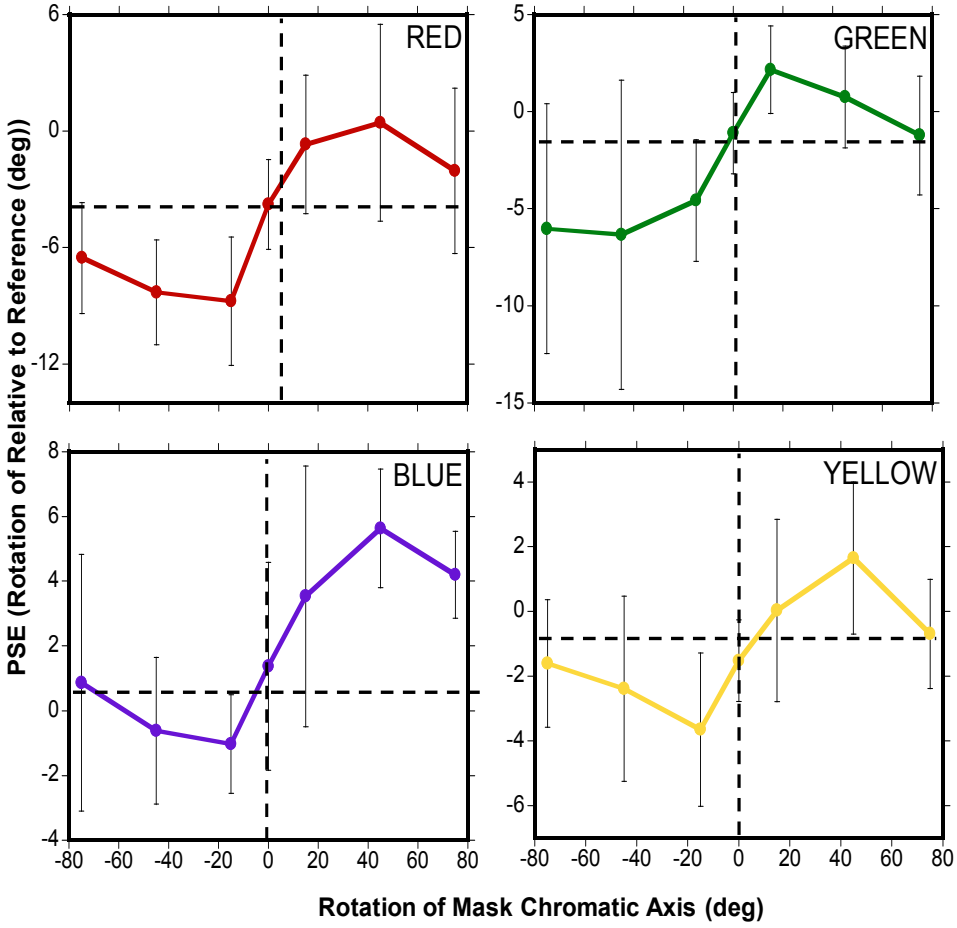


Figure 5.4 Averaged PSE values from five observers. PSE values plotted as a function of relative mask rotations. The colours of the markers indicate the reference colour. Dashed horizontal lines indicate averaged baseline performance of five observers, vertical dashed lines represent the reference colour.

The tuned nature of these masking effects on PSEs prompted us to further examine whether the effect of the mask is localised to a specific region of colour space. One reference colour was examined (blue) for two of the observers for the full range of mask colours. PSE values were plotted as a function of relative mask rotation as before (**Figure 5.5**). As previously shown, the effect of the mask seems to only occur within a certain range centred on the reference stimulus.

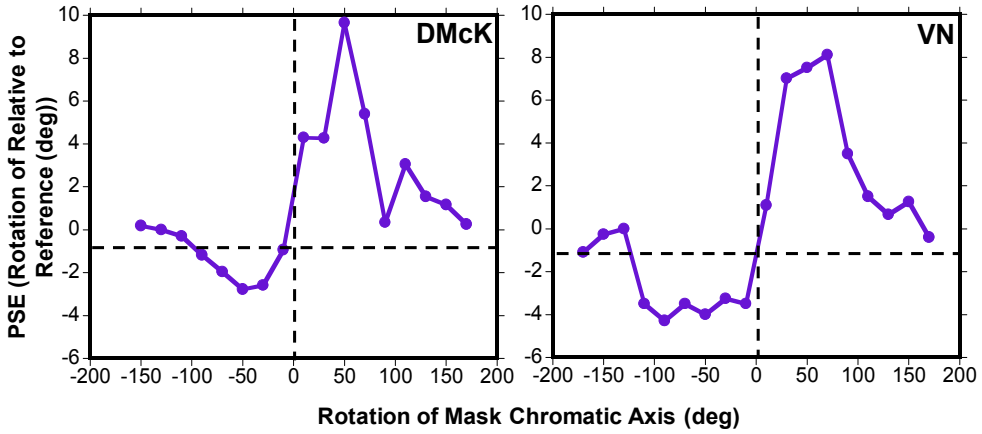


Figure 5.5 Hue shift (PSE) values plotted as a function of relative mask rotations. Data from two observers for the reference hue blue. Horizontal dashed lines indicate baseline performance, vertical dashed lines represent the reference colour.

Overall, we found a consistent pattern, in that the colour matches made by the observers are highly dependent upon the chromaticity of the masking stimulus. The findings we present here seem to indicate that masking effects are restricted to certain regions of the colour space. The pattern of these results overall suggests that the mask stimulus can interfere with the stored representation of the colour of the reference stimulus and can induce a shift in the point of perceived equality as long as the mask colour is different, but not too different, from the reference stimulus. Thus it would appear that memory masking for colour exhibits tuning or selectivity similar to that which has already been demonstrated as existent for other visual attributes such as motion and spatial frequency (Magnussen et al., 1991; McKeefry et al., 2007).

The selective pattern of the masking effects gave us the incentive to fit the data with first derivative of Gaussian functions which allowed us to derive an estimate for the bandwidth (σ = standard deviation of the Gaussian) of these masking effects (see **Chapter 3**, **Section 3.7.2.3**). The results of this fitting procedure are shown in **Figure 5.6** where the group averaged data (n = 5) for each reference stimulus colour have been fitted by these functions. The

resulting values for the bandwidths of the masking effects were: 34.093° for the red reference stimulus, 33.428° for the green, 29.047° for the yellow and 36.794° for the blue.

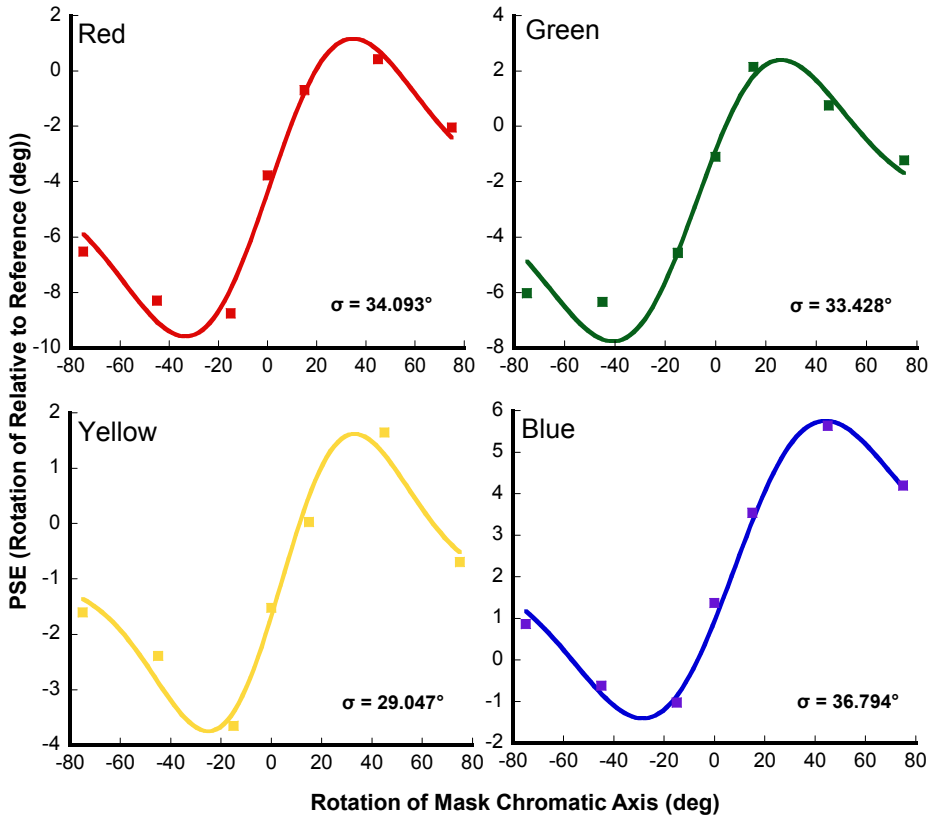


Figure 5.6 Averaged PSE data for the five observers fitted with the 1st derivative of a Gaussian function. The bandwidths (standard deviation of the Gaussian) of each curve fit are indicated on the graphs.

It has already been demonstrated that subcortical colour mechanisms have a bandwidth of 60° and narrower bandwidths indicate the presence of non-linear higher order mechanisms (Clifford et al., 2003; Goda & Fujii, 2001; Kiper et al., 1997). Similar bandwidths for the perceptual hue and hue memory masking mechanisms would confirm that both take place at or beyond the level of V1. Since one of our questions was whether VSTM mechanisms for colour are connected to higher order cortical areas, we decided to, in the next step, compare the bandwidth of the masking effects with the bandwidth of the

perceptual colour mechanisms. In order to do this, we fitted a Gaussian function to the averaged colour naming data that was presented in **Chapter 4** (**Section 4.2**), to get an estimate of the bandwidth and to compare these with the bandwidths of the hue memory masking functions. The results of the Gaussian curve fitting procedures in comparison with the first derivative of the Gaussian are shown in **Figures 5.7**, and **5.8** for the group averaged data (n = 5) for each reference stimulus. As can be seen, in case of blue, red and green, the distribution of the data was not normal, since it had a wide a plateau, indicating the range of colours the observers chose 100% of the time as belonging to the same colour category. For this reason, the Gaussian curve fits had to be modified for the hue scaling data in order to get a reliable estimate of the bandwidth. In case of these curve fits, a bandwidth is calculated as the sum of the half width of the plateau and half width of the curve at half height.

The σ values that were obtained from the Gaussian fits of the hue naming functions reveal bandwidths of 42.923° and 28.886° for blue and yellow, respectively (**Figure 5.7**). These bandwidths are of comparable magnitude with the ones obtained from colour memory masking experiments and are also comparable to non-linear, higher order colour mechanisms. This serves as evidence that the storage of chromatic information in VSTM might be organised based on perceptual colour categories. However, we found some discrepancy in case of the bandwidth estimates between memory masking and the hue naming data for the red and green reference stimuli. The hue naming functions for red and green yield much broader bandwidths of 64.029° and 60.084°, respectively (**Figure 5.8**). This discrepancy might have arisen as a consequence of the hue scaling method we used, which limited the observers to use one of the four basic colour terms to describe each stimulus (red, green,

blue and yellow) and resulted in broader functions. It is well known that there are more than four colour discrimination mechanisms (De Valois et al., 1997b; Goda & Fujii, 2001), therefore there is a possibility that each of these broader colour categories comprises further sub-categories with narrower bandwidths that would have shown more similarities with the results of the memory masking.

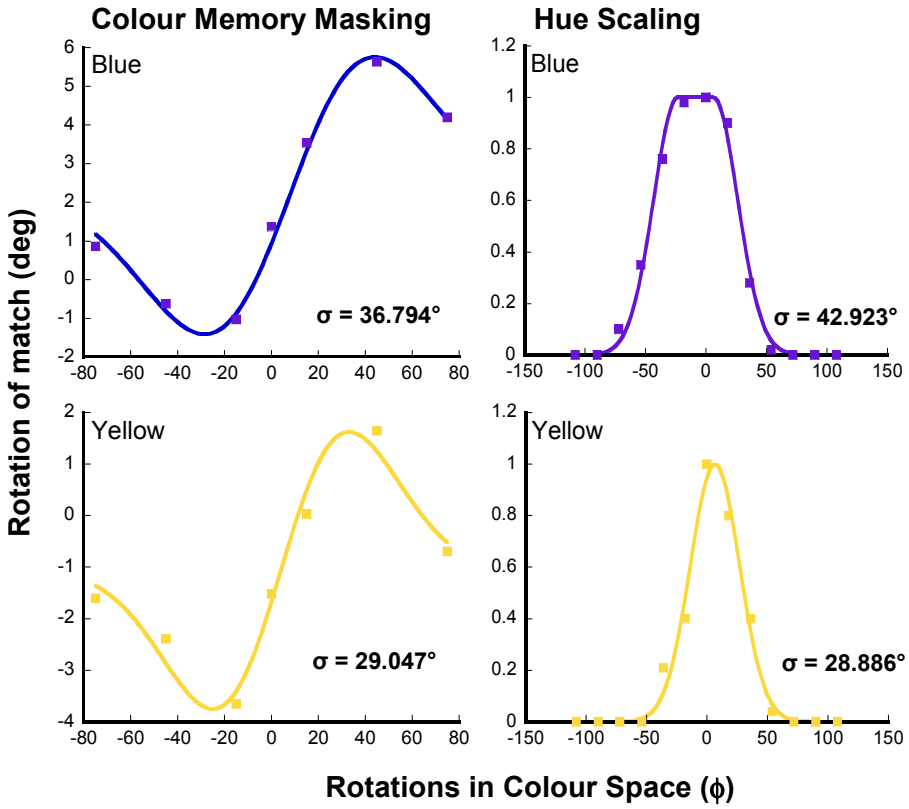


Figure 5.7 First column: averaged PSE data for the five observers fitted with the 1st derivative of a Gaussian function, Second column: Hue naming functions fitted with a Gaussian model. The bandwidth values of the best fitting functions (standard deviation of the Gaussian) are indicated on the individual plots for comparison. In case of the colours blue and yellow, the bandwidths show a great deal of similarity.

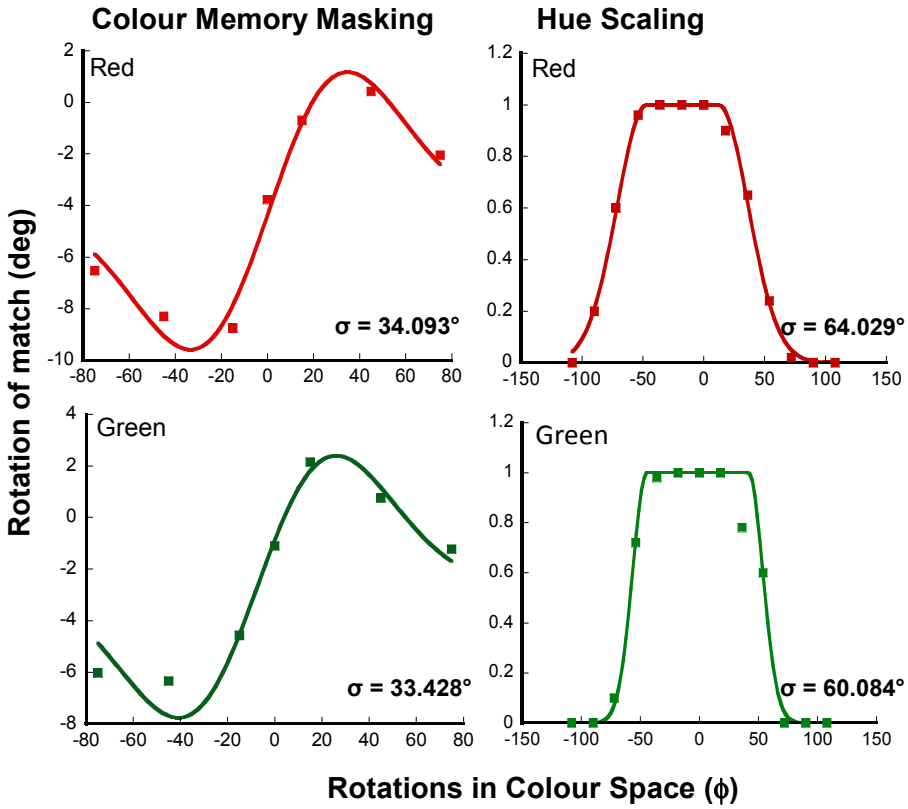


Figure 5.8 First column: averaged PSE data for the five observers fitted with the 1st derivative of a Gaussian function, Second column: Hue naming functions fitted with a Gaussian model. The bandwidth values of the best fitting functions (standard deviation of the Gaussian) are indicated on the individual plots for comparison. The bandwidth values for the memory masking and the hue naming data are not directly comparable.

5.2.4 Discussion

In this study we have demonstrated, using a delayed colour discrimination paradigm, the existence of selective, hue dependent, mask induced interference effects on stored representations of colour stimuli within VSTM. This finding is consistent with previous studies that have demonstrated similar selectivity for other visual attributes in VSTM (Bennett & Cortese, 1996; Lalonde & Chaudhuri, 2002; Magnussen et al., 1991; McKeefry et al., 2007). The results suggest that colour, like other visual attributes can call upon a dedicated memory mechanism that can store information related to this dimension. Similar to other visual attributes (Magnussen, 2009), perceptual memory for colour appears to

contain an array of stores that holds chromatic information across relatively limited bandwidths of colour space.

If we hypothesise that a given memory mask is only effective if its colour is similar, but not equal to the reference colour, than we assume that the effectivity of a mask depends on it being in the same category. In this case, the bandwidth of the memory masking effect provides indirect information about the bandwidth of the sensory mechanisms for the basic hue categories upon which VSTM for colour might be based. Since colour naming data is based upon perceptual hue categories, the bandwidth (σ) of these functions provides us information regarding the bandwidth of the colour mechanisms at higher cortical levels, at which, processing of colours is most likely organized according to the perceptual colour categories (Conway, 2003; De Valois et al., 2000a; De Valois & De Valois, 1993; Xiao et al., 2007; Xiao et al., 2003). It has already been shown that there is a narrowing in terms of the colour tuning from the cone opponent to the perceptual colour processing at some cortical level. In the LGN (Derrington et al., 1984) and V1 (De Valois et al., 2000a; Lennie et al., 1990), neurons have a broad tuning of 60° that is related to linear summed cone inputs. This is due to the fact that cone-opponent neurons rely upon linear combinations of L-, M- and S-cone inputs and exhibit responses to colour stimuli across MBDKL colour space that vary in a cosinusoidal (L-M) or sinusoidal (S-(L+M)) fashion (De Valois et al., 2000a; Derrington et al., 1984). However, in the cortex there seems to be a narrowing of the chromatic tuning (Clifford et al., 2003; Kiper et al., 1997). For these reasons, comparison of the bandwidths of the memory masking effects and the perceptual colour processing mechanisms provides us with valuable information regarding the organization of colour information in VSTM. Similarities in the bandwidths of

perceptual colour mechanisms and memory masking effects would serve as indirect evidence that both take place at higher cortical levels. The bandwidth of the memory masking effect across colour space fell between 29° and 37° for the stimuli tested. The extent of this tuning is narrower than what might have been expected if these interference effects were mediated by neurons that received cone-opponent input. Instead, the bandwidths of the memory masking effects reported here are more typical of those that have been found for higher-order colour mechanisms which rely upon non-linear cone inputs and have reported bandwidths of approximately 40° (Goda & Fujii, 2001; Kiper et al., 1997). The bandwidth values we acquired from these memory masking experiments are well below 60°, therefore imply the involvement of higher order mechanisms in VSTM, possibly at, or higher than the level of V1 or V2 (**Figure 5.6**) (Clifford et al., 2003; De Valois et al., 1997b; Goda & Fujii, 2001), where the transformation from cone-opponent to more perceptually relevant colour coding has taken place.

Recent neuro-imaging studies have indicated that the transformation from cone-opponent to more perceptually based colour processing occurs at the level of visual areas VO1 (ventral occipital) and V4 (Brouwer & Heeger, 2009). Thus these areas might constitute a possible locus for the neural activity that underpins short term perceptual colour memory. Certainly, area V4 has long been viewed as playing an important role in colour processing (Lueck et al., 1989; McKeefry & Zeki, 1997a; Zeki, 1980). Its involvement in colour perceptual memory, along with neighbouring areas in the ventral extra-striate cortex, would be consistent with views of perceptual memory being based upon neural activity based within a network of brain areas located beyond V1, but relatively early in the cortical processing stream (Fuster, 1997; Magnussen, 2009; Offen

et al., 2009). Furthermore, neural activity in area V4 has been strongly linked to mechanisms of storage in visual short term memory (Sligte et al., 2009).

In summary, using memory masks of different hues in a delayed matching paradigm, we have found hue dependent mask induced interference effects that serve as evidence for colour selectivity in VSTM. The data suggests that there might be separate memory stores that hold information about perceptual colour categories in VSTM. We attempted to compare the bandwidth of the memory masking data and the bandwidth of the hue naming mechanisms and we have, in some cases found evidence for more narrowly tuned mechanisms indicating that VSTM for colour might exploit higher-order non-linear colour mechanisms.

5.3 The Effect of Saturation and Luminance Contrast on Short Term Colour Memory

5.3.1 Introduction

It has been a matter of debate whether colour and luminance information are processed via common or separate sensory pathways (Livingstone & Hubel, 1988). Results of experiments that employed sensory masking (De Valois & De Valois, 1993; Gegenfurtner & Kiper, 1992; Mullen & Losada, 1994; Switkes et al., 1988), contrast detection threshold measurement (Gegenfurtner & Kiper, 1992) and adaptation methods (Bradley et al., 1988; Krauskopf et al., 1982) concluded that colour and luminance information are processed independently of each other in visual perception.

In most cases simultaneous changes in colour and luminance do not increase discrimination thresholds in a delayed discrimination task, which supports the separate processing theory (Greenlee et al., 1997; Yoshizawa et al., 2011).

However, some of the experiments examining the organisation of colour and luminance information in VSTM still assumed that the processing is interconnected at higher cortical levels but not at the level of V1 (Cornelissen & Greenlee, 2000), an idea which was also confirmed by lesion studies (Greenlee et al., 1997). Using luminance masking noise, Yoshizawa et al. (Yoshizawa et al., 2011) found evidence that luminance signals do not interfere with the storage of colour information, which further confirms the separate processing theory.

The aim of this study was to examine to what extent visual perceptual memory displays selectivity for stimulus colour and luminance. We used the memory masking paradigm in order to assess the extent to which chromaticity, saturation and luminance content of a masking stimulus can interfere with the fidelity of the stored representation of colours. It has been shown in the previous section (**Section 5.2**), that there is a colour specific masking effect in tasks examining memory for colour and we wanted to further investigate whether the same holds for saturation and luminance. Stimulus selectivity for saturation and luminance would provide evidence for their separate processing in VSTM (i.e. no interference effects), which would mirror the way they are probably organised in sensory processing (Magnussen et al., 1996; Nilsson & Nelson, 1981; Sachtler & Zaidi, 1992; Yoshizawa et al., 2011).

Moreover, implicit in our stimulus design is the assumption that equal length vectors in MBDKL colour space generate stimuli which have the same perceived saturation. This is not a valid assumption in view of the perceptual non-uniformity of this colour space. In order to demonstrate that these colour memory masking effects were not simply the result of differences in perceived

saturation of the masking stimuli, we examined these effects by varying their saturation.

5.3.2 Methods

The effect of increasing saturation of the mask hue was examined first. Stimuli were sharp edged circular patches that subtended 1.5° visual angle. The exemplars of the unique hue blue (ϕ_{DM} = 126° and ϕ_{VN} = 117°) were chosen as references and were matched with the corresponding test hues that spanned a range $\phi = \pm 21°$ after a 5 s long time delay. Masks of two different hues were employed, which were chosen based on the previous colour memory masking experiments; one was similar to the reference colour and caused the greatest PSE shift (ϕ = +34° relative rotation to the reference) and one that was very different from the reference colour and caused minimal PSE changes as compared to baseline performance (ϕ = +108° relative rotation to the reference) (**Figure 5.9**). Saturation levels of the mask stimuli that were employed in the different runs varied between 0 and 150% (0, 25, 75, 100, 150%) (**Figure 5.10**). Changing saturation levels in MBDKL colour space were represented by the variable lengths of the hue vectors (ϕ) on the isoluminant plane of colour space (**Figure 5.10**). These stimuli had similar luminance levels and were equiluminant with the background. Each reference and one of the corresponding test stimuli were presented ten times and the hues of the test stimuli were varied in a random order to avoid any learning effect. The reference and test stimuli were separated horizontally, the reference was displayed 1.5° to the right of the fixation point, and the test was presented 1.5° to the left of fixation mark along a horizontal line. The mask stimulus was presented on the centre of the screen. Baseline performance data was collected

in the absence of a masking stimulus (**Figure 5.2**). As previously, a delayed hue discrimination paradigm was employed (see details in **Section 5.2**) and the observers were asked to indicate the perceived hue of the test stimulus relative to the reference in MBDKL colour space.

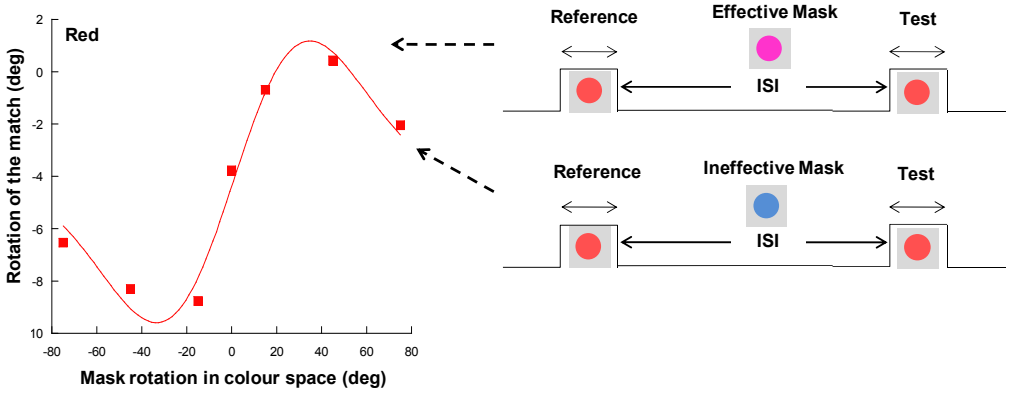


Figure 5.9 Illustration of mask hue selection in the saturation masking experiments. Based on the results of **Section 5.2** mask hues that caused either maximal change (an effective mask) or minimal change (an ineffective mask) were selected. Different saturation levels of these masks were then employed in the different runs.

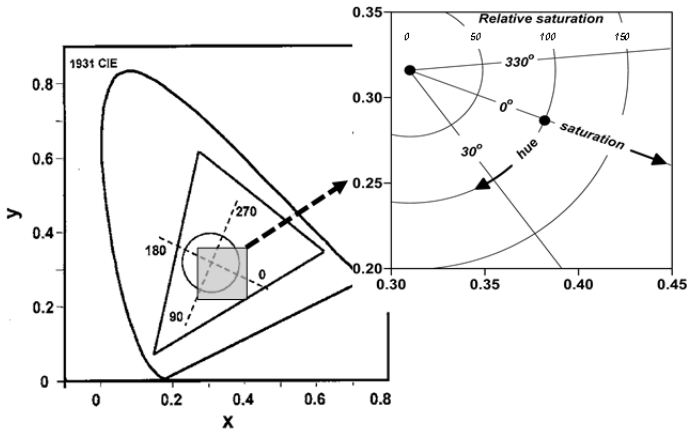


Figure 5.10 Illustration of stimulus saturation. Changes in saturation of a certain hue are represented by changes of the length of the vector that represents the hue on an isoluminant plane in MBDKL colour space.

In case of the luminance ratio experiments, the reference stimulus represented the exemplar of the red perceptual colour category ($\phi_{DM,VN}$ = 18°) and it was compared with the corresponding range of test colours as described previously

in this chapter (**Figure 5.1** and **5.2**). One mask hue was selected based on the previous experiments, which caused the greatest perceived hue shift in memory (ϕ = +34° relative rotation to the reference) (**Figure 5.9**) (see **Section 5.2**). Changes in luminance represent changes in MBDKL colour space perpendicular to the isloluminant plane, i.e. elevation from the isoluminant plane (**Figure 3.5**). The luminance contrast content of the mask stimuli were manipulated by variation of their luminance ratio (LR) which was defined as:

$$LR = \frac{L_{ms}}{L_{ms} + L_{bg}} \quad (5.1)$$

Where; L_{ms} = luminance of masking stimulus and L_{bg} = luminance of background. An LR=0.5 generates a mask stimulus that is photometrically equiluminant with the background (i.e. contains only chromatic contrast). Values either side of this generate stimuli containing varying amounts of luminance and chromatic contrast, with luminance increments denoted by LR>0.5 and decrements by LR<0.5 (**Figure 5.11**).

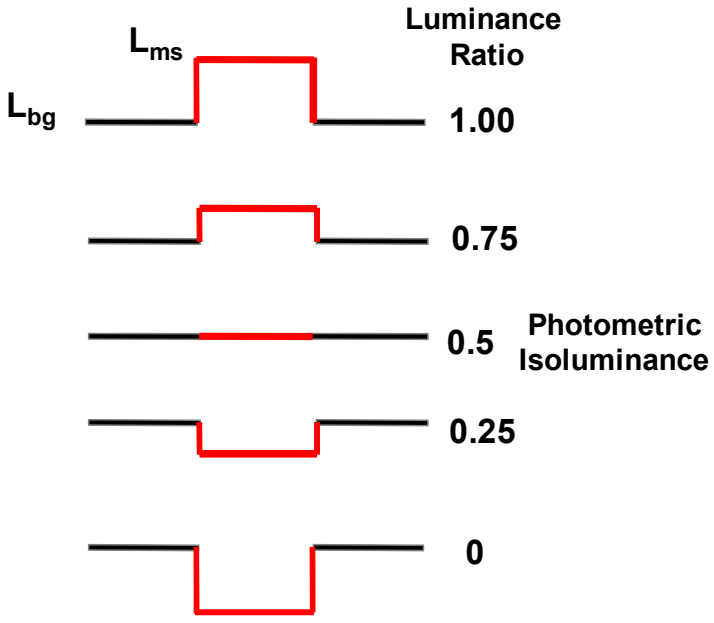


Figure 5.11 Luminance profiles of uniform coloured stimuli. The black lines correspond to the background luminance (L_{bg}) and the red lines symbolize the luminance of the square wave

stimuli (L_{ms}). An isoluminant stimulus is defined by a luminance ratio of 0.5, and increasing and decreasing luminance ratios define non-isoluminant stimuli.

The background, reference and test stimulus luminance in all cases was 12.5 cd/m^2 and the mask luminance ratios (ratio of the stimulus luminance level divided by the sum of the background and stimulus luminance) were set to values of 0.1, 0.25, 0.4, 0.5 (isoluminance), 0.6, 0.75 and 0.9, where a luminance ratio of 0.5 represented the condition where the mask stimulus and the background had the same luminance level. In terms of luminance levels these values were the following: 1.39 cd/m^2, 4.17 cd/m^2, 8.33 cd/m^2, 12.5 cd/m^2, 18.75 cd/m^2, 37.5 cd/m^2 and 112.5 cd/m^2. As described previously, a delayed hue discrimination paradigm was employed with the same conditions as in the saturation experiments (see **Section 5.2** for details).

As before, the psychometric data were fitted by a logistic function and PSE values were extracted and plotted as a function of mask saturation and luminance (for details see **Section 5.2**).

Two experienced observers took part in these experiments (1 female and 1 male; mean age = 39 years). Both had normal colour vision according to Rayleigh matches made on a HMC Anomaloskop and the Farnsworth-Munsell 100-Hue test. Both had 6/6 or corrected to 6/6 Snellen visual acuity. The experiments were performed in a darkened room and observers fixated on a small black cross on the centre of the screen which was viewed binocularly from a distance of 114 cm.

5.3.3 Results

PSE values were plotted as a function of mask saturation in **Figure 5.12**. The red data points represent the resulting PSE values for the effective mask and

the blue points indicate a cross category (ineffective) mask that was very different (**Figure 5.12**). The graphs demonstrate that changes in mask saturation levels had an effect on the perceived hue of the retained stimulus only when the employed mask belonged to the 'effective' group, whereby increasing mask saturation results in increasingly larger shifts in PSE, away from the actual reference hue. Ineffective masks had minimal effect on the PSE obtained from this experiment, and this is the case regardless of their saturation. i.e. an ineffective mask cannot be made effective simply by increasing its saturation over the same range where the effective mask has a gradually increasing effect. This implies that a more saturated mask hue shifts the stored representation of the reference colour to a greater extent, resulting in greater PSE values. In the case where the mask was 'ineffective', increasing saturation levels had little or no effect on the PSE.

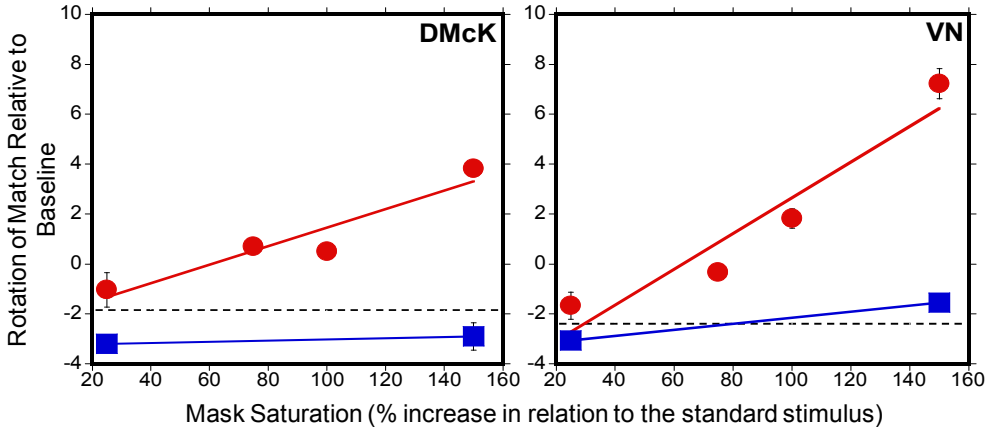


Figure 5.12 Results of the hue saturation experiment. PSE values plotted as a function of mask saturation levels. Individual data is presented, error bars represent errors of the curve fits. Horizontal dashed lines indicate 'without-mask' baseline performance.

Figure 5.13 shows PSE values plotted as a function of mask luminance ratios. In this case an effective, within category mask was chosen that has the ability to selectively disrupt the retention of the exemplar hue red in VSTM. According to the data, the worst performance is centred at a luminance ratio of 0.5 (where

mask and background were at isoluminance), where the perceived shift of the retained colour is the greatest. Lower and higher luminance values of the stimuli have a gradually decreasing effect on the PSE. When luminance contrast is added to the mask and LR increases or decreases from a value of 0.5, PSEs fall to levels similar to those obtained for the no mask condition. Thus, the addition of luminance contrast to masking stimuli makes them less effective in their ability to interfere with the retention of chromatic information.

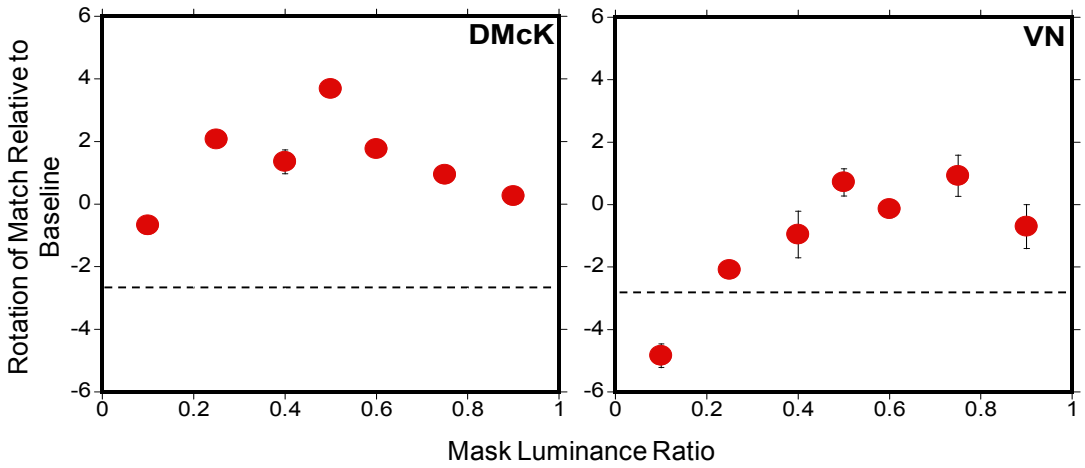


Figure 5.13 Results of the luminance ratio experiments. PSE values plotted as a function of mask luminance ratios. Individual data is presented, error bars represent errors of the curve fits. Horizontal dashed lines indicate 'without-mask' baseline performance.

5.3.4 Discussion

In these experiments the organisation of colour, saturation and luminance information in VSTM was examined, by changing the saturation and luminance levels of the interfering stimulus while information about hue had to be retained in memory. We have found stimulus selectivity for the saturation and luminance content of the remembered colour. We assumed that stimulus specific interference would occur if the two types of information are processed by a common mechanism. We have found that in cases when the reference and the mask stimuli are similar, increasing mask saturation leads to a gradually

worsening performance, as measured by the increase in the perceived shifts in memory. This might imply that within each separate hue storage, there are further separate storage mechanisms that are devoted to the representation of saturation (i.e. chromatic content). The increasing masking effect was not present in case of an ineffective mask that had a very different colour from that of the reference, which could serve as further evidence in favour of the existence of parallel channels in VSTM, each devoted to the storage of individual perceptual hue categories.

Our results show, that the most prominent memory masking effect occurs when the stimuli are at isoluminance and mask stimuli of higher or lower luminance levels result in their gradually decreasing effect. In case when the luminance ratio approaches 0 or 1 the effect of the mask diminishes and approached baseline, as if in that case the visual system is able to ignore the stimuli. This tends to suggest that luminance and colour are connected at some cortical level in perceptual short term memory.

There is a limited amount of information regarding the characteristics of perceptual memory for saturation and luminance in the literature. Memory for saturation has been examined in a successive matching experiment (Uchikawa, 1983), where observers had to remember the saturation of coloured stimuli for 3 s. Compared to simultaneous matching, a decrease in the ability to discriminate different saturation levels in memory was shown. Moreover, remembered colours tended to shift towards more saturated colours, i.e., a more saturated test colour was matched as being of equal saturation to the reference one. Others also concluded that the retained saturation level increases in memory

(Newhall et al., 1957) although some did not find this effect (Hanawalt & Post, 1942).

In order to estimate the accuracy of memory for luminance, Uchikawa and Ikeda (Uchikawa & Ikeda, 1986) examined delayed matching performance (ISI = 2 s) for coloured lights of different brightness levels and found that discrimination thresholds were more variable compared to simultaneous matching. There was also a shift in the memory representation of the perceived brightness, darker colours were remembered as darker, whereas brighter colours were remembered as being brighter, which is in agreement with previous results (Newhall et al., 1957).

Yoshizawa and colleagues (Yoshizawa et al., 2011) examined sensory memory for colour and luminance employing a 200 ms ISI. They masked the memory representation of colours with luminance masks and concluded that the two do not interact in memory, luminance masks do not appear to interfere with colour representations. Variation of luminance ratios did not lead to any change either. Since memory represents early processing, they assumed that this serves as evidence that luminance and colour do not interact in low level processes, which is in agreement with earlier results (Mullen & Losada, 1994; Sachtler & Zaidi, 1992; Switkes et al., 1988). Sachtler and Zaidi (Sachtler & Zaidi, 1992) found that memory for colour was more accurate than for luminance in a delayed discrimination task. In their experiment, they measured delayed discrimination ability for chromatic and luminance stimuli and found that colour was better retained as compared to luminance signals (i.e. at equal cone excitations colour was more efficient than luminance in memory). Compared to

simultaneous discrimination, successive discrimination ability of luminance signals was less accurate than in case of chromatic signals.

One advantage of separate storage mechanisms for luminance and colour information would be hue invariance, which allows the individual to recognise objects independent of colour, or despite changes in the illuminant. In a sensory masking experiment, Switkes et al. (Switkes et al., 1988) examined colour and luminance interactions in sensory processing and found that the detection of colour was facilitated by luminance masking but the detection of luminance was attenuated by chromatic masks. Therefore it can be assumed that there is some interaction depending on the stimulus characteristics. There is evidence in the literature that memory for colour is more accurate than memory for luminance (Sachtler & Zaidi, 1992) and that luminance information is stored separately from colour (Cornelissen & Greenlee, 2000). According to Cornelissen and Greenlee, performance in memory for colour and luminance is similar (Cornelissen & Greenlee, 2000). They hypothesised that in case of colour and luminance, information is stored in different storage mechanism, therefore there should be no change in performance when both change during a task. Whereas if they belong to the same mechanism then if both change at the same time there should be a decrease in performance. Bearing this in mind, their results served as evidence that there are separate memory mechanisms that are responsible for the storage of luminance and colour contrast information.

In conclusion, in these experiments we have examined interactions between hue, saturation and luminance information in VSTM employing a memory masking paradigm. We have shown that increasing mask saturation levels resulted in increasingly larger PSE shifts in cases of effective masks (masks

that had similar colour to that of the reference), whereas ineffective masks (masks that had very different colours from the reference) did not have an effect on PSE values. Luminance contrast content had an effect on the performance, namely, adding luminance contrast information to the masking stimuli resulted in their decreased ability to interfere with the stored representation of the memory colour. We believe that we have found stimulus selectivity for saturation and luminance in VSTM for colour. This finding supports the view of separate information storage mechanisms for different types of visual information in perceptual memory.

5.4 General Discussion

In this chapter our aim was to investigate the organisation of colour information in VSTM. In order to do this, we have examined stimulus selectivity for colour, saturation and luminance and we have found evidence for stimulus selectivity and separate storage mechanisms for these attributes.

We have demonstrated the existence of selective, hue dependent, mask induced interference effects on stored representations of colour stimuli within short term visual perceptual memory. This finding indicates that colour perceptual memory contains an array of stores that hold chromatic information across relatively limited bandwidths of colour space. The narrow tuning of these memory masking effects suggests that the neural mechanisms that underpin these interferences effects are located at a stage in visual processing where there has been a transformation of chromatic processing away from cone-opponency towards more perceptually relevant colour coding mechanisms. Consistent with previous studies, colour memory masking effects are ‘tuned’ in

the respect that perceived hues of the retained stimuli are unaffected when the reference and mask hues are identical, but increase as the mask hue shifts away from the reference hue, in terms of hue, saturation or luminance ratio.

Our data is consistent with earlier studies, which examined the representation in memory of colours with specific interest in the eleven perceptual colour categories (Uchikawa & Shinoda, 1996). In the case when two colours are similar, they are more easily confused in memory, as compared to two colours that belong to different colour categories. This is in agreement with the results of Boynton et al. who found that the colour categories indeed have an effect on accuracy, in a delayed matching task, colours that belong to the same colour category were more difficult to accurately discriminate from each other in a memory task (Boynton et al., 1989). This serves as evidence that the memory representation of colours is organised on the basis of the main perceptual colour categories. One possible explanation for this could be that colours are categorized in memory in order to be better retained and subtle differences between colours that belong to the same category are more difficult to be discriminated in memory.

It is highly likely, that different colour groups are represented by different groups of neurons which serve as a basis of organisation of information in VSTM (Magnussen, 2000; Magnussen & Greenlee, 1999). The selective nature of colour memory masking effects suggests that within VSTM, similar to other basic visual attributes, there are separate memory stores for different perceptual colour categories within which the representation of information is relatively coarse. The results presented here can be interpreted by the noisy exemplar model (Kahana & Sekuler, 2002). This model assumes that the

memory representation is imperfect due to noise, and the storage of memoranda takes place in multiplex, individual memory representations. Based on this, in VSTM for colour, each perceptual colour category is represented in separate storage as a summed similarity value of a collection of hues that give a normal distribution in colour space around the main colour. So each colour could be represented by a pool of similar colours and their summed similarity is what is compared with the test stimuli in the memory task. The response of the individual depends on an internal criterion level; if the difference between the summed similarity of the internal representation and the test colour exceeds the internal criterion level, then the hues are perceived as different (Kahana & Sekuler, 2002). If colour information is represented as summed similarities and is subject to perceptual modification, than the most recently seen colours could affect the summed similarity the most, so it might be the case that in the masking condition, similar colours that are presented after the reference are able to shift the memory representation (Kahana & Sekuler, 2002).

In summary, in this chapter, we carried out experiments in order to examine the organization of colour information in VSTM for hue, saturation and luminance employing a memory masking paradigm. We assessed the fidelity of the memory representation by measuring changes in PSE. PSE values showed a mask hue specific alteration pattern and these effects revealed narrowly tuned mechanisms that to a certain extent show correlation with perceptual colour mechanisms. We have found stimulus specific mechanisms for hue, luminance and saturation in VSTM for colour and these findings were interpreted as evidence for the existence of similarities between sensory and memory processes in the analysis of colour.

Chapter 6

Investigation of Multiple Spatial Frequency Channels in Human Visual Short Term Memory

6.1 Introduction

Recent evidence shows that visual perceptual memory is closely associated with the sensory analysis of visual information and may even occur in the same cortical areas (Bisley & Pasternak, 2000; Fuster, 1997; Gibson & Maunsell, 1997; Pasternak & Greenlee, 2005). In the visual domain, the retention of information about basic attributes, such as spatial frequency, motion, contrast and so forth has been shown to occur within what is termed as a low-level perceptual memory system (Magnussen, 2000; Magnussen & Greenlee, 1999). A key property of visual perceptual memory is that it is dimension specific. It comprises a series of parallel memory stores that are selective for the retention of specific visual attributes such as spatial frequency, orientation, colour, speed, etc. (Magnussen & Greenlee, 1999; McKeefry et al., 2007; Pasternak & Greenlee, 2005). Such an organisation mirrors that found right from the earliest stages in the visual pathway, where the sensory processing of different stimulus attributes occurs in a similarly parallel fashion (Livingstone & Hubel, 1988).

Memory for spatial frequency has been traditionally examined using a two-interval forced choice procedure, employing ISIs between the reference and test stimuli that range between 0 - 30 s (Magnussen et al., 1990; Magnussen et al., 1991; Magnussen et al., 1996; Magnussen et al., 1998). The quality or fidelity of the retained information is indexed by changes in performance such as discrimination thresholds and perceived spatial frequency shifts. Memory for spatial frequency in a delayed discrimination task has been found to be highly accurate (Magnussen et al., 1990; Magnussen et al., 1991; Magnussen et al., 1998). According to these studies, simultaneous and delayed discrimination thresholds are similar, suggesting they are underpinned by the same mechanisms.

Evidence for feature specificity in visual perceptual memory has also emerged from the psychophysical studies. Using this approach, the retention of different stimulus features (contrast, orientation, spatial frequency, vernier offset etc.) has been found to have different rates of decay with increasing ISI, suggesting that different perceptual memory mechanisms exist for different attributes (Fahle & Harris, 1992; Lee & Harris, 1996; Magnussen & Greenlee, 1999; Magnussen et al., 1996; Magnussen et al., 1998; Vogel et al., 2006). Feature specificity has also been demonstrated by the selective effects of interference or masking stimuli presented during the ISIs of delayed discrimination tasks (Magnussen et al., 1991). In these so-called ‘memory masking’ experiments increases in discrimination thresholds induced by the introduction of masking stimuli point to the ability of certain stimuli to disrupt the retention of information about specific stimulus features. An important property of memory masking is that the effects are specific to changes only along certain relevant stimulus dimensions with discrimination thresholds being unaffected by changes along

other irrelevant dimensions. Furthermore, the effects are also tuned for finite ranges of these features (Magnussen et al., 1991). The disruptions to stored representations of visual stimuli only occur when the interfering or masking stimuli differ from the remembered stimulus in some key aspect, there is no disruption of performance when the mask is identical to the reference (Magnussen & Greenlee, 1992; Magnussen et al., 1991; McKeefry et al., 2007).

Adaptation experiments have shown that an adaptor grating of high contrast results in perceived shifts of the test stimulus, and the direction of these shifts depends on the spatial frequency of the adaptor (Blakemore et al., 1970). These experiments further confirmed the idea that there are multiple spatial frequency channels in sensory processing (see **Chapter 1**, **Section 1.2.6**) (Blakemore & Campbell, 1969a, 1969b; Blakemore & Nachmias, 1971; Blakemore et al., 1970; Campbell & Robson, 1968; Georgeson & Harris, 1984).

In this chapter we intended to initially replicate previous results of Magnussen (Magnussen et al., 1991; Magnussen et al., 1996) in order to demonstrate the effect of the mask on the discrimination thresholds and furthermore to examine changes in terms of the perceived spatial frequency shifts (PSEs). We assumed that specific changes in the point of subjective equality (PSE) would confirm that in VSTM the representation of information is organized in a similar way to sensory processing. We attempted to examine VSTM for spatial frequency in the view of the existence of multiple spatial frequency channels in sensory processing. We wished to further elucidate the link between visual sensory processing and visual perceptual memory. Following on from this we examined the effect of basic stimulus parameters such as spatial location, contrast and

orientation in order to further establish characteristics of the VSTM for spatial frequency.

6.2 The Retention of Spatial Frequency in Visual Short Term Memory

6.2.1 Introduction

In this study a memory masking paradigm was used to investigate how spatial frequency information is organised within visual perceptual memory. Perhaps one of the most enduring models of low-level visual processing describes the analysis of spatial patterns in terms of the parallel operation of multiple spatial frequency filters or channels (Campbell & Robson, 1968). Experiments using pattern or contrast adaptation have played a major role in characterising these low-level sensory filters which are responsive to specific bandwidths of frequency and orientation and operate in separate spatial locations (Blakemore & Campbell, 1969b; Blakemore & Nachmias, 1971; Blakemore et al., 1970; Georgeson & Harris, 1984). Memory masking experiments have made an analogous contribution in revealing the organisation of perceptual memory for spatial frequency. Magnussen et al. (Magnussen et al., 1991), for example, have demonstrated that visual perceptual memory does exhibit spatial frequency tuning, which mirrors that found in low-level vision. This finding has been central to the proposition that such memory stores are closely linked to the mechanisms that operate at the earliest stages of sensory processing (Magnussen, 2009; Magnussen et al., 1991; Pasternak & Greenlee, 2005).

In this study we aimed to examine whether low-level perceptual memory consists of multiple spatially tuned mechanisms similar to those which have

been revealed in the sensory domain using adaptation and sensory masking paradigms (Blakemore & Campbell, 1969a; Blakemore et al., 1970; Campbell & Robson, 1968). Evidence for the existence of multiple spatially tuned channels would further strengthen the case for visual perceptual memory being closely allied to low-level visual processing. In addition, we also wanted to assess the extent to which the effects of memory masking are localised relative to the positions of the mask stimuli in order to gauge the extent to which these filters can interact across different spatial locations in perceptual memory. In order to examine this, two conditions were compared in this study, in the first, the reference, mask, and test presentation locations coincided, whereas in the second they were spatially separated.

6.2.2 Methods

Sinusoidal luminance contrast grating stimuli were presented on a colour graphics monitor (GDM500; Sony, Tokyo, Japan; frame rate 120Hz) controlled via a video graphics card (VSG 2/5; Cambridge Research Systems, Rochester, UK). The reference, mask and test stimuli were presented in circular windows of 2.5° diameter, with a contrast equal to 50% on a grey (illuminant C) background of the same mean luminance (12.5 cd/m^2) (see **Figure 6.1**). The reference stimuli had spatial frequencies of 1, 3 or 5 c/deg, the corresponding test spatial frequencies spanned a given range above and below the reference spatial frequency, at seven different levels, optimized individually in order to yield a smooth psychometric function. Mask spatial frequencies represented a range within ± 2 octaves of the reference spatial frequency. A detailed description of the stimulus structure and display can be found in **Chapter 3** (**Sections 3.3.2** and **3.6.2**).

A delayed spatial frequency matching paradigm (**Figure 6.1**) was used to measure performance, and employed a two-alternative forced choice procedure in conjunction with a method of constant stimuli. Each trial began with the presentation of a reference stimulus for 380 ms. This was followed by an inter-stimulus interval of 5 s, during which masking stimuli of different spatial frequencies were presented for 2 s. At the end of the ISI a test stimulus was presented for 380 ms. The offset of the test stimulus was marked by an auditory cue at which point the participants were required to indicate, using a response box (model CB3; Cambridge Research Systems), whether the test stimulus was perceived to be of higher or lower spatial frequency than the reference. In order to prevent the representation of stimulus features being built up in long-term memory over consecutive trials we introduced small random increases and decreases (jitter) in the contrast (between $\pm$ 10%) and spatial phase (between $\pm$ 90°) of the test and reference stimuli.

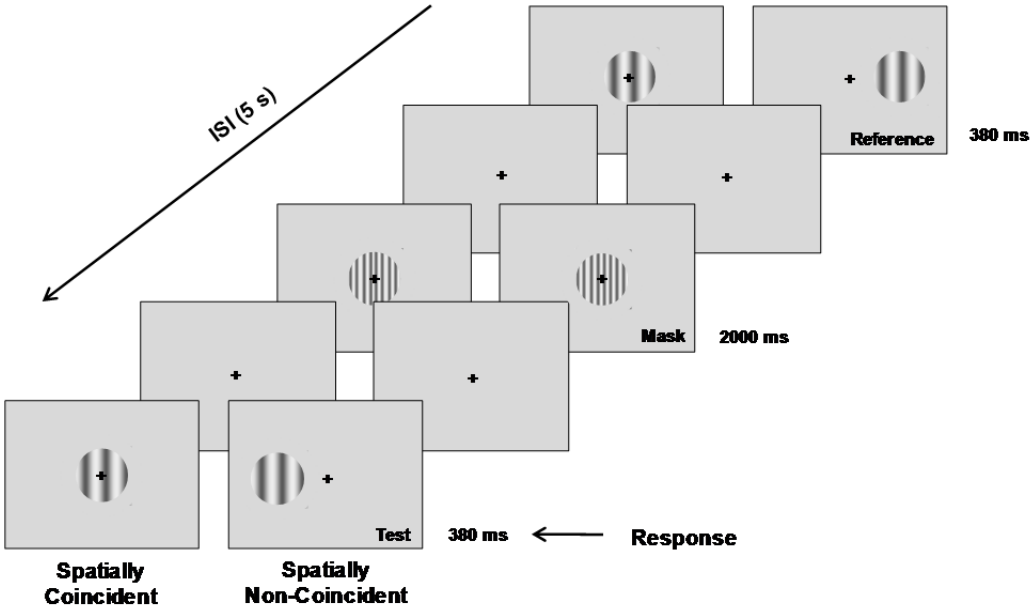


Figure 6.1 A schematic representation of the delayed spatial frequency discrimination paradigm used in this study. Each cycle began with the presentation of a reference stimulus (1, 3 or 5 c/deg) for 380 ms. Following the presentation of a blank screen for 1500 ms a mask stimulus was displayed for 2000 ms. After another 1500 ms ISI, a test stimulus appeared for 380 ms, after which the observer had to make a response by a button press indicating whether they judged the test to be of higher or lower spatial frequency than the reference stimulus. Following the response the next presentation cycle began. There were two forms of the experiment: A) a spatially coincident version where the reference, test and mask stimuli were all presented at the same spatial location centred on the fixation point and B) a spatially non-coincident version where the stimuli were horizontally displaced form one another by distances of up to 6°.

In terms of the spatial configuration of the stimuli two versions of the same experiment were performed; in the first, spatially coincident version, the reference, mask and test stimuli were all presented at the same spatial location centred on the fixation point. In the second, spatially non-coincident version, the reference stimulus was presented with a horizontal displacement to the right of the central fixation mark; the mask stimulus was displayed at the fixation mark and the test stimulus was placed to the left of fixation. The magnitude of the displacements from the fixation point varied up to a maximum of 6°. During the presentation cycle fixation was maintained on a central fixation cross.

Altogether three observers took part in the study (1 female and 2 males; mean age = 36 years, S.D. = ±8.66 years), two of whom were experienced observers and one was naive as to the aims of the experiment. All gave informed consent

and had 6/6 or corrected to 6/6 Snellen visual acuity. The experiments were performed in a darkened room and observers fixated on a small black cross on the centre of the screen which was viewed binocularly from a distance of 114 cm.

The behavioural data were fitted by a logistic function of the form and the resulting PSE values were plotted as a function of mask spatial frequency and fitted with the first derivative of the Gaussian function (see **Chapter 3**, **Section 3.7.2.3**).

6.2.3 Results

Figure 6.2 illustrates the group averaged results from an experiment where participants performed the delayed spatial frequency matching task for a reference stimulus of 5 c/deg in the presence of different mask stimuli ranging between 1 - 15 c/deg. **Figure 6.2A** shows how discrimination threshold varies as a function of the mask spatial frequency. In these experiments we replicated the memory masking paradigm of Magnussen et al., (Magnussen et al., 1991) and demonstrated spatial frequency selectivity in terms of the effects on discrimination thresholds and PSEs. When the mask spatial frequency is close to that of the reference stimulus, performance is minimally affected and thresholds are similar to those obtained when no mask is presented during the ISI (horizontal dashed line on the graphs). However, as the mask spatial frequency starts to shift away from that of the reference, either towards lower or higher values, then thresholds increase giving rise to a characteristic 'V-shaped' function that is approximately centred on the reference spatial frequency.

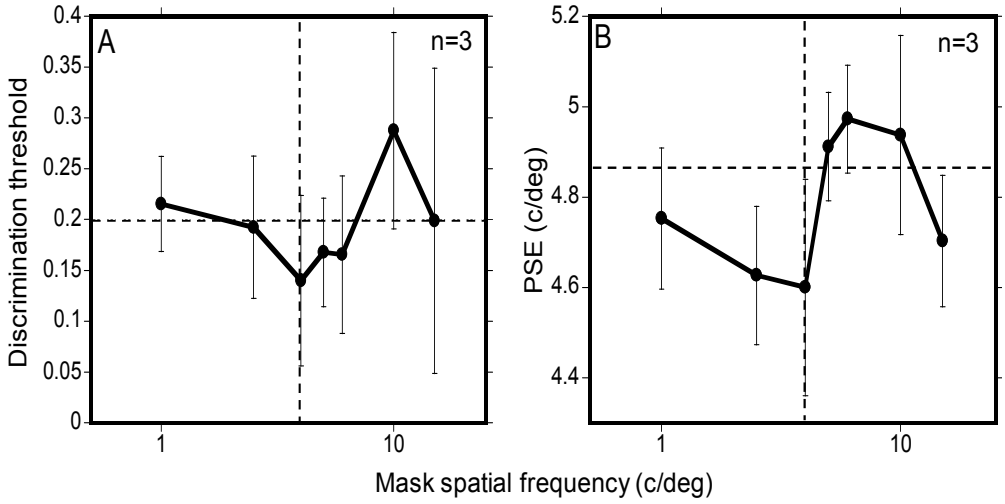


Figure 6.2 Group averaged results (n=3) for a delayed spatial frequency discrimination experiment (references = 5 c/deg) where mask stimuli of variable spatial frequency were presented during the 5 s ISI. The graphs plot how A) discrimination thresholds and B) PSEs vary as a function of mask spatial frequency. In this and subsequent plots the horizontal dashed line refers to the level of (baseline) performance when no mask stimulus was introduced during the ISI. The vertical dashed line represents the references spatial frequency and error bars refer to ± SD of the mean.

In addition to plotting how discrimination thresholds vary, our methodology also allows us to plot how PSE varies as a function of mask spatial frequency. This is shown in **Figure 6.2B** where PSEs can be observed to vary in a characteristic manner relative to the baseline condition (i.e. when no mask is present). For mask spatial frequencies below that of the reference, perceived equality between reference and test occurs at spatial frequencies that are lower than the baseline PSE. Conversely, when the mask frequency is greater than the reference, PSE values are greater than for the baseline condition. Either side of the reference spatial frequency the perceived shift in the PSE reaches a local maximum for higher mask frequencies and local minimum for lower mask frequencies. When the mask spatial frequency moves even further away from the reference the perceived shifts in the PSE decrease in magnitude and return back towards baseline values. Thus the perceived shifts in the matched spatial frequency appear highly dependent upon the spatial frequency of the masking

stimuli. If the mask spatial frequency differs by a small amount from the reference stimulus, the resultant PSE is 'pulled' towards the spatial frequency of the mask stimulus. If, however, the difference between the reference and mask spatial frequency becomes too great then the effect is reduced and the PSE starts to return to values closer to those obtained under no mask conditions, as if a substantially different mask stimulus can be ignored by the visual system.

The spatially tuned nature of these PSE changes prompted us to fit this initial experimental data with first derivatives of Gaussian functions (see **General Methods, Sections 3.7.2.3**). These functions have the advantage of offering an estimate of the bandwidth of the effects in terms providing a value (σ = standard deviation of the Gausian function). **Figure 6.3** shows results obtained from three individual observers whose data have been fitted with these functions that give values of σ = 0.545, 0.455 and 0.638 octaves (bandwidth) for observers DMcK, VN and FF, respectively. Based on this characteristic tuning pattern, we decided to further investigate the perceived shifts that arise as a result of the memory mask stimulus in order to explore stimulus selectivity for spatial frequency in VSTM.

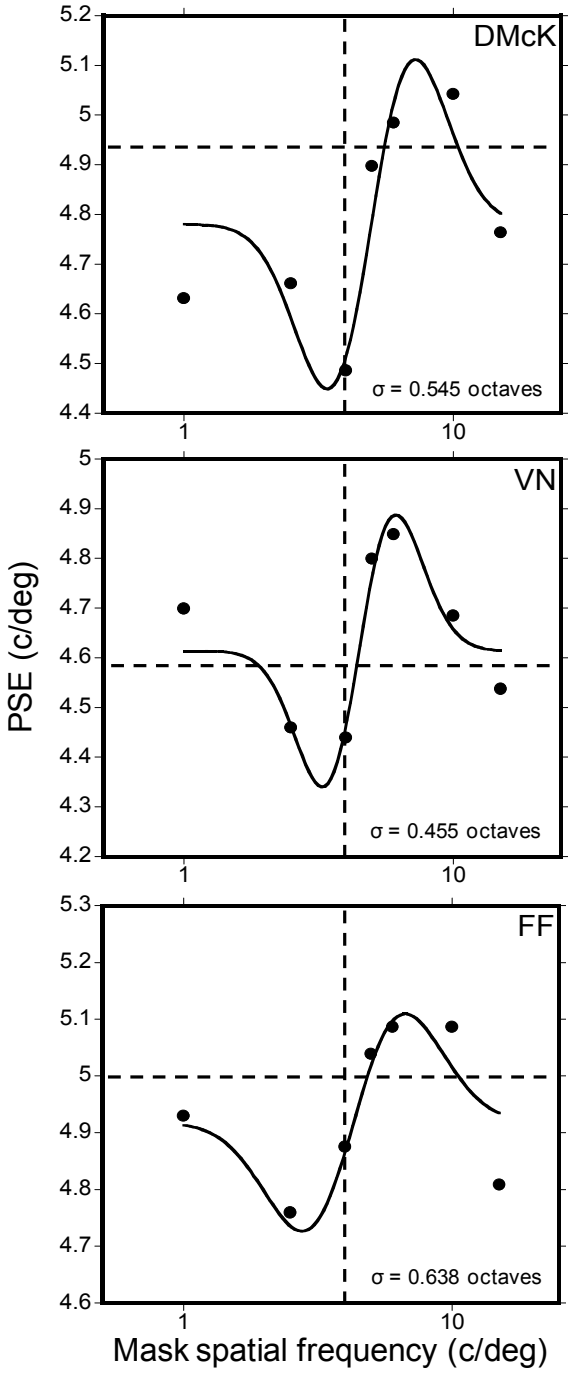


Figure 6.3 PSE data plotted as a function of mask spatial frequency for three observers who performed a delayed spatial frequency matching paradigm (reference = 5 c/deg). The data have been fitted by the first derivative of a Gaussian function which provides an estimate of bandwidth (σ = standard deviation of the Gausian) for each function given in spatial frequencies.

Figures 6.4-6.10 show memory masking data for two observers for reference spatial frequencies 1, 3 and 5 c/deg in spatially coincident and separated conditions. Individual and averaged PSE values were plotted as a function of mask spatial frequency for the two observers (**Figures 6.4** - **6.6**) for the spatially

coincident and the spatially separated conditions (**Figures 6.7** - **6.9**). The data were fitted with the first derivative Gaussian functions. For every dataset the same characteristic pattern of memory masking emerges as described before. Minimal masking effect can be observed when the mask had either the same spatial frequency as the reference or was substantially different from it. Within these extreme points the mask causes a consistent shift in the perceived spatial frequency of the test, which occurs towards the spatial frequency of the mask, i.e., the memory shift in the matched spatial frequency is dependent on the spatial frequency of the mask. For example, when the mask spatial frequency is higher than that of the reference, the matches made by the observers are 'pulled' in the same direction as the mask, away from the baseline value, i.e. they will be made at higher spatial frequencies.

The findings seem to indicate that masking effects are restricted to certain spatial frequency ranges. The pattern of these results overall suggests that the mask stimulus can interfere with the stored representation of the spatial frequency and can induce a shift in the point of perceived equality as long the mask spatial frequency is different, but not too different, from the reference stimulus. Thus it would confirm the previous findings, that memory masking for spatial frequency exhibits tuning or selectivity (Magnussen et al., 1991; McKeefry et al., 2007).

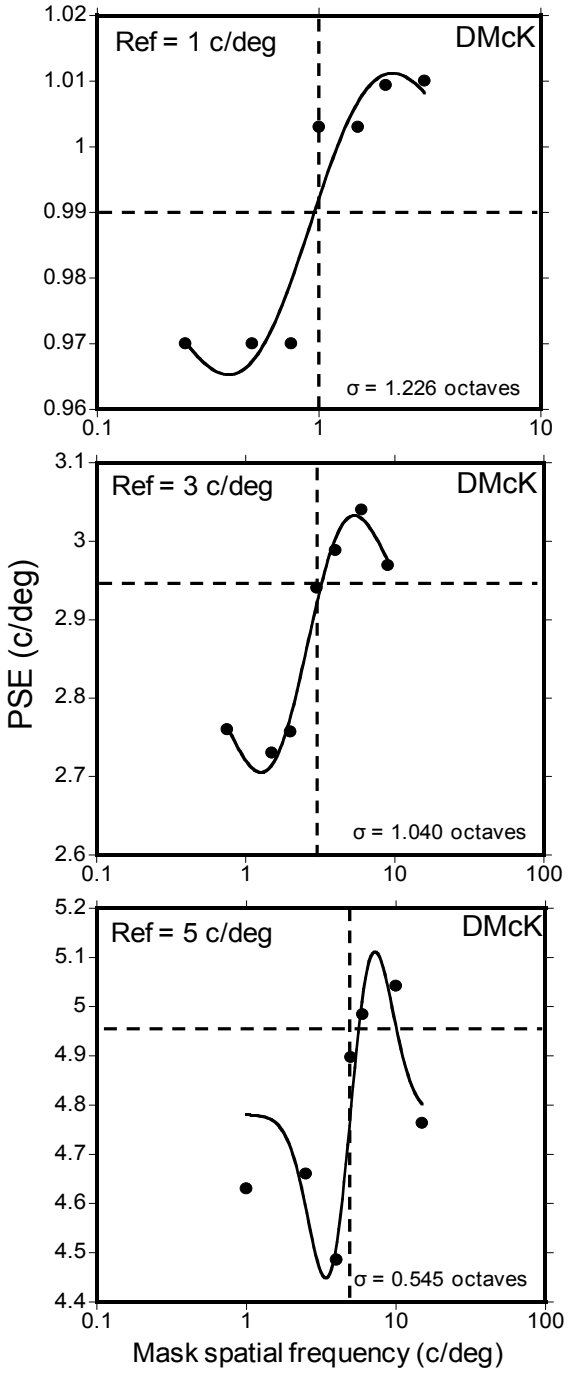


Figure 6.4 Variation in PSE as a function of mask spatial frequency for three different reference spatial frequencies (1, 3 and 5 c/deg) in the spatially coincident condition. The data in each case is from an individual observer (DMcK) and have been fitted by a first derivative of a Gaussian function.

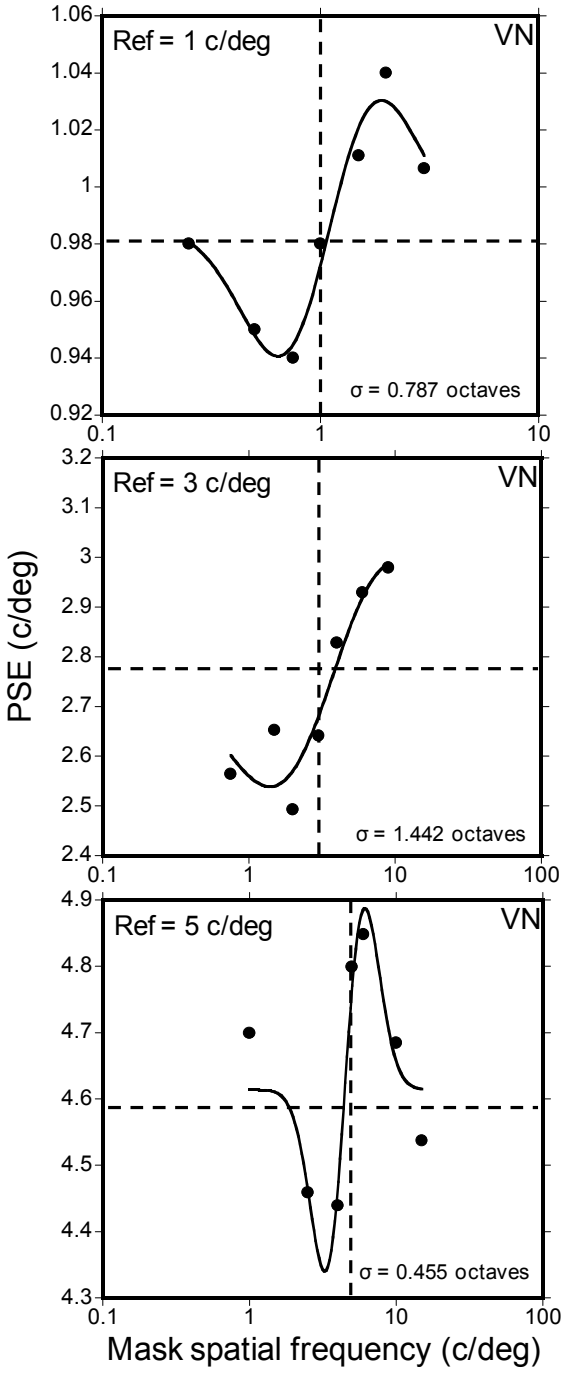


Figure 6.5 Variation in PSE as a function of mask spatial frequency for three different reference spatial frequencies (1, 3 and 5 c/deg) in the spatially coincident condition. The data in each case is from an individual observer (VN) and have been fitted by a first derivative of a Gaussian function.

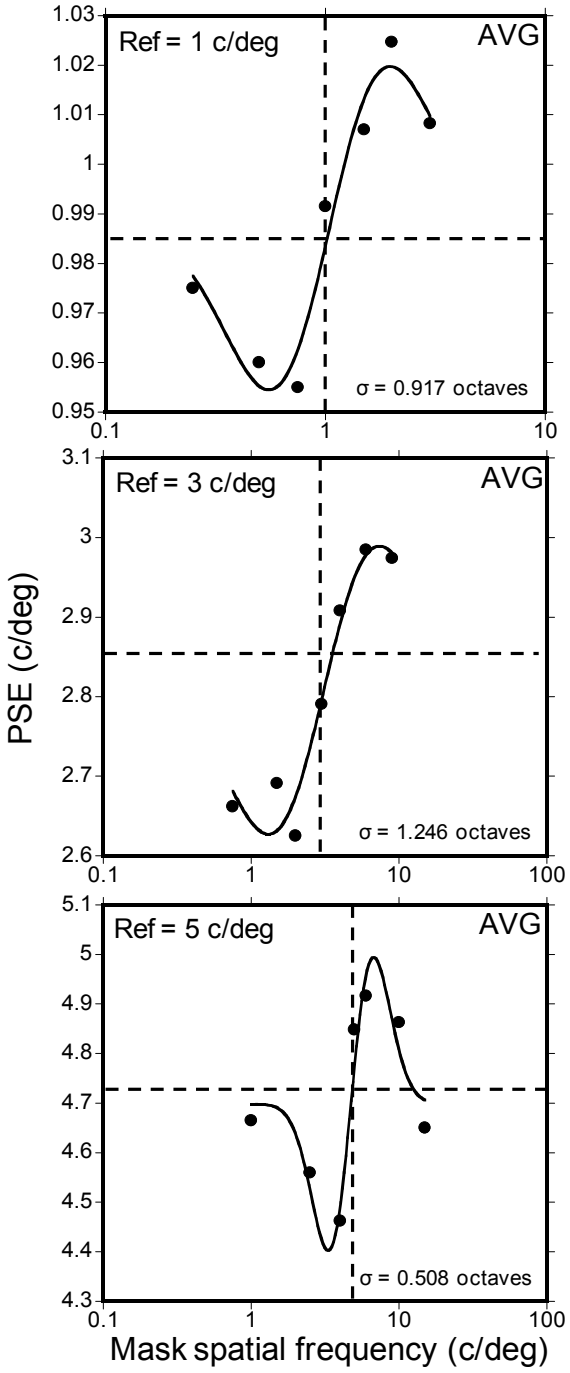


Figure 6.6 Averaged data replotted from **Figures 6.4** and **6.5**. Variation in PSE as a function of mask spatial frequency for three different reference spatial frequencies (1, 3 and 5 c/deg) in the spatially coincident condition. The data in each case represent the average of two observers and have been fitted by a first derivative of a Gaussian function.

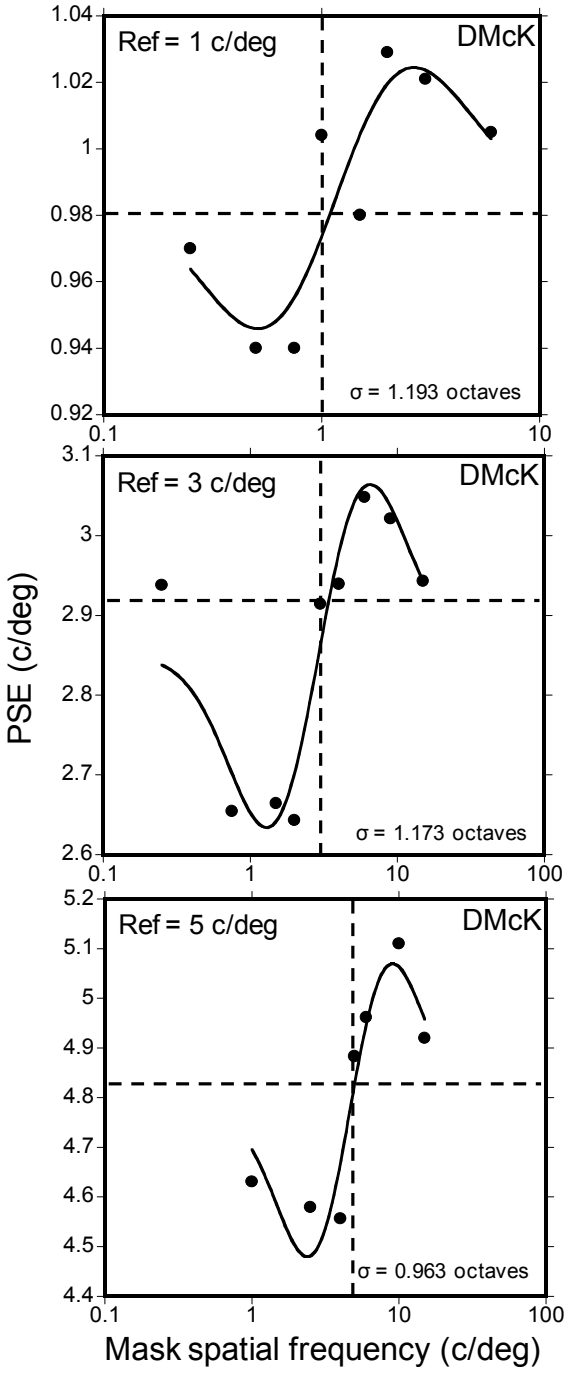


Figure 6.7 Variation in PSE as a function of mask spatial frequency for three different reference spatial frequencies (1, 3 and 5 c/deg) in the spatially separate condition. The data in each case is from an individual observer (DMcK) and have been fitted by a first derivative of a Gaussian function.

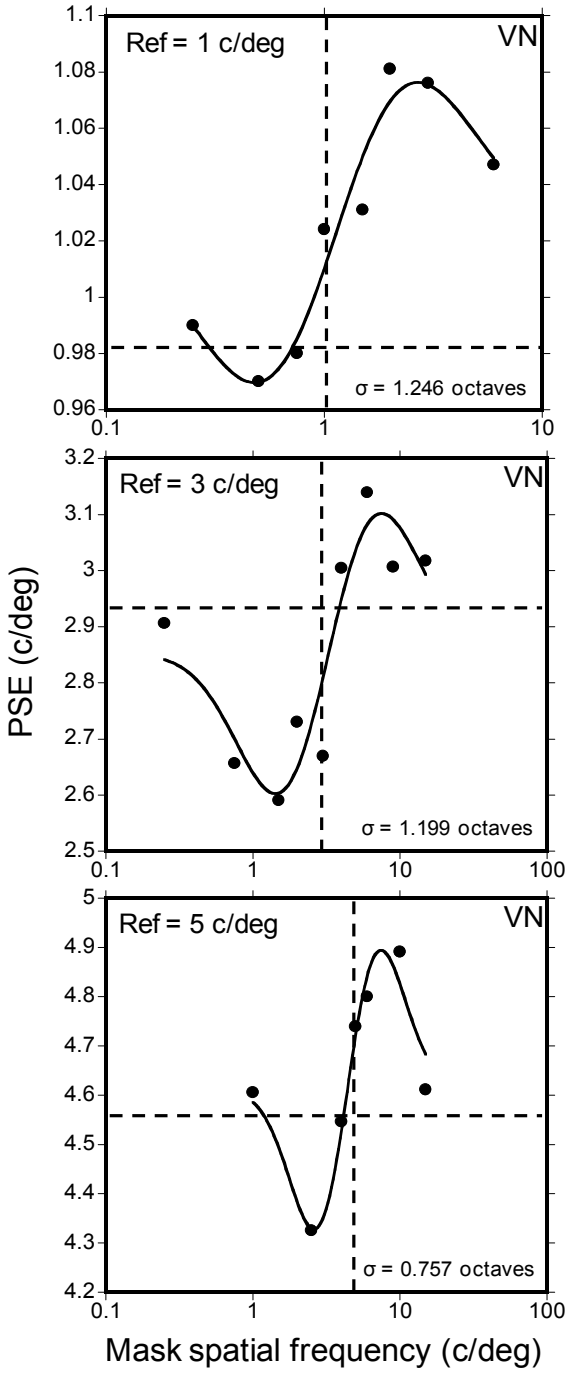


Figure 6.8 Variation in PSE as a function of mask spatial frequency for three different reference spatial frequencies (1, 3 and 5 c/deg) in the spatially separate condition. The data in each case is from an individual observer (VN) and have been fitted by a first derivative of a Gaussian function.

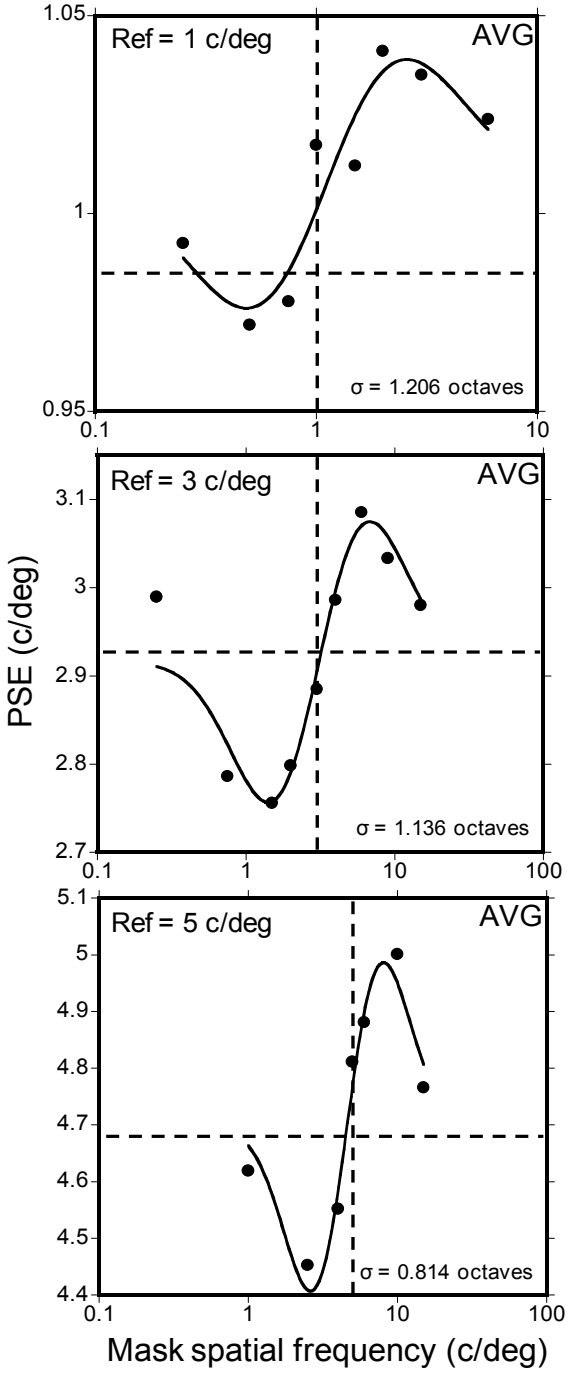


Figure 6.9 Averaged PSE data replotted from **Figures 6.7** and **6.8**. The data shows the variation in PSE as a function of mask spatial frequency for three different reference spatial frequencies (1, 3 and 5 c/deg) in the spatially separate condition. The data in each case represent the average of two observers and have been fitted by a first derivative of a Gaussian function.

The spatial frequency selective effects demonstrated here using the 'memory masking' paradigm mirror the kind of effects that also occur in contrast or pattern adaptation experiments (Blakemore et al., 1970). In these experiments, prolonged exposure to a particular spatial frequency alters the perceived

frequency of subsequently viewed grating stimuli. Results from these adaptation experiments have been central to the formulation of models of spatial vision processing that rely upon the existence multiple filters or channels that are responsive to relatively narrow spatial frequency bandwidths. In **Figure 6.10** data from Blakemore et al. (Blakemore et al., 1970) have been re-plotted in order to show how the perceived spatial frequency of various test stimuli vary following prolonged exposure to either a 3 c/deg or a 5 c/deg (**Figure 6.10**) grating. As in the case of the 'memory masking' data shown before (**Figure 6.4-6.9)** these contrast adaptation data have been fitted by first derivatives of Gaussian functions which generates values of σ = 0.60 octaves for the 3 c/deg data and σ = 0.66 octaves for the 5 c/deg data.

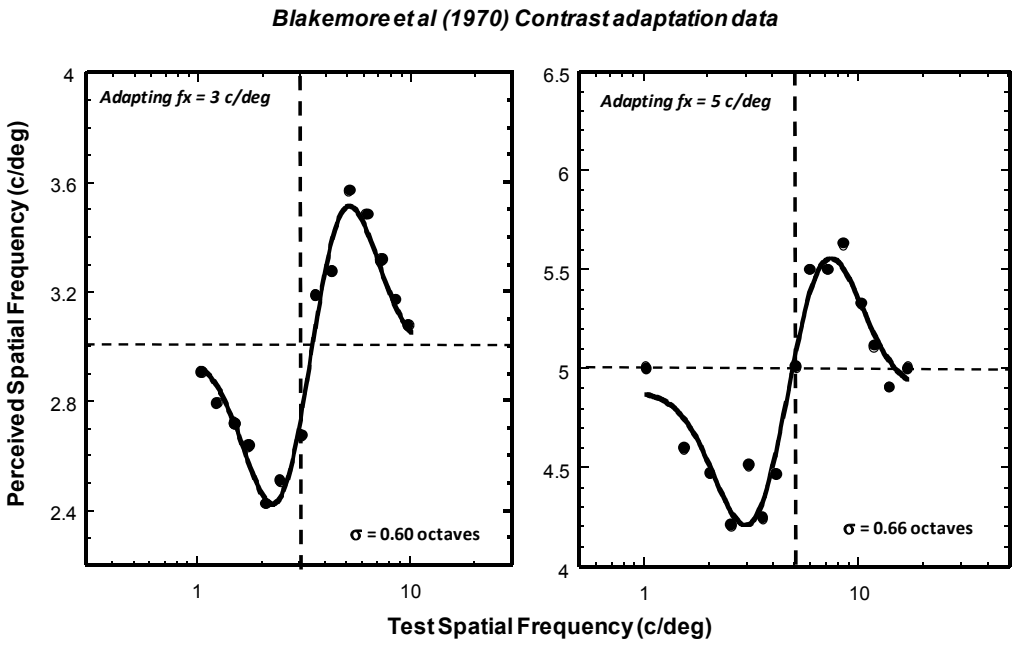


Figure 6.10 Contrast adaptation data from Blakemore et al. (Blakemore et al., 1970) which demonstrate the variation in perceived spatial frequency of test stimuli following prior adaptation to a 3 c/deg (A) and a 5 c/deg (B) grating stimulus. The data have been fitted with the first derivative of a Gaussian function.

Whilst the spatial bandwidths of the contrast adaptation and memory masking effects are of comparable magnitude in most cases, there are, on the other hand, important differences between the two effects. One such difference lies in

the extent to which the respective effects are spatially localised. **Figures 6.7 - 6.9** show the results from a delayed spatial frequency matching task where the reference, mask and test stimuli appeared in different locations in the visual field with no overlap in the location (see **Figure 6.1**). The centres of each stimulus were separated horizontally by 3° and as can be observed the effects of the different masking stimuli exhibit similar spatial frequency tuning to that found when the reference, mask and test stimuli were spatially co-incident. Data in **Figure 6.11** show that perceived shifts in matched spatial frequency for a reference stimulus of 3 c/deg that are induced by effective masks (1.5 and 6 c/deg) still occur for stimulus separations up to 6° without any diminution in magnitude. This non-spatially localised property of memory masking differs markedly from that exhibited by contrast adaptation (Blakemore & Campbell, 1969a).

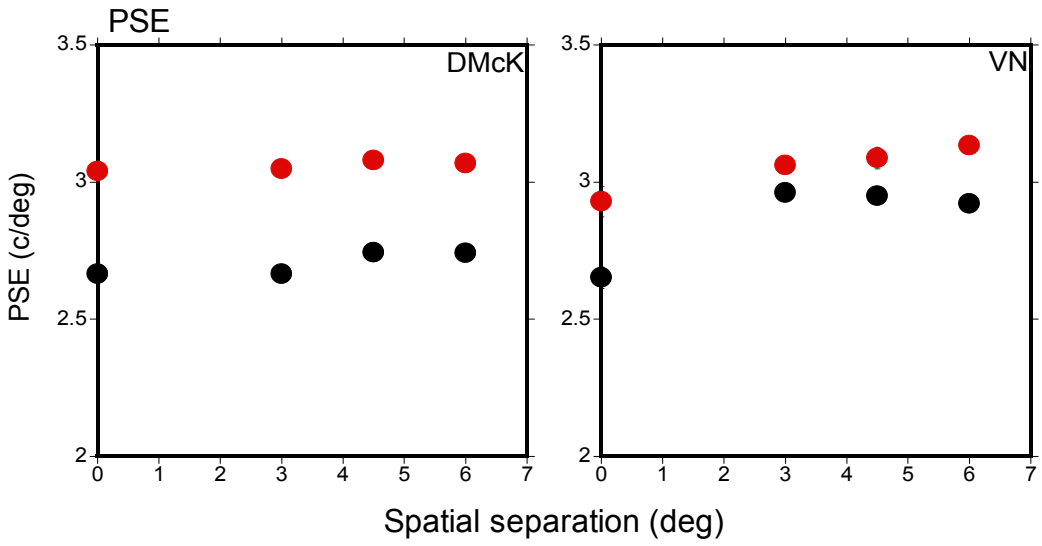


Figure 6.11 Shifts in PSEs for spatial frequency matches made for a 3 c/deg reference stimulus with masking stimuli (6 c/deg: red dots, and 1.5 c/deg: black dots) placed at increasingly larger horizontal separations (coincident, 3°, 4.5° and 6°).

6.2.4 Discussion

The purpose of these experiments was to investigate the proposed links between visual sensory processing and visual perceptual memory. Using a delayed spatial frequency discrimination task that employed a memory masking paradigm we were able to measure the accuracy with which visual stimuli were retained by perceptual memory mechanisms and assess the effects the interfering stimuli had on the fidelity of the memory store. Our central finding is that masking stimuli were able to shift PSEs for matches made by observers between the reference and test stimuli, as long as their spatial frequency was within a bandwidth of approximately 1.2 – 2.5 octaves, centred on the reference spatial frequency. When mask spatial frequencies differed by more than this amount, the PSEs changed little or not at all from baseline levels. In the case of the memory masking the PSE values are consistently shifted in the same direction as the effective mask, they are attractive in nature i.e. higher spatial frequency masks shift the reported PSE towards higher spatial frequencies than the actual reference, whilst an effective mask of lower spatial frequency shifts PSE values to lower frequencies. This selective pattern of masking was observed for reference stimuli of various spatial frequencies and demonstrates the existence of multiple, spatially tuned mechanisms in visual perceptual memory.

The existence of multiple spatially tuned mechanisms in low-level perceptual memory is in accord with those models which describe perceptual memory as comprising an array of stores that are able to retain information about a particular stimulus dimension within only a limited range or bandwidth (Magnussen, 2000, 2009; Magnussen & Greenlee, 1999; Magnussen et al., 1991). The masking bandwidths we have measured for different reference

spatial frequencies range between 0.45 - 1.4 octaves for the spatially co-incident versions of the paradigm and between 0.76 - 1.25 octaves for the non-coincident versions. These bandwidths revealed by memory masking are in good agreement with those obtained from sensory adaptation paradigms (Blakemore et al., 1970), which in turn are similar to those that have been measured in primate V1 neurons. DeValois et al. (De Valois et al., 1982a) for example, have shown that the range of bandwidths exhibited for macaque foveal V1 neurons is between 0.7 - 2.5 octaves. The consistency between the tuning bandwidths displayed by perceptual memory mechanisms and visual neurons in V1 implies that the former are closely linked to sensory discrimination properties of the latter (Magnussen, 2009). Thus, it would appear that the neural mechanisms that serve to retain spatial frequency information in perceptual memory adhere to similar organisational principles as those exhibited by the sensory filters that are involved in the earliest visual analysis of this information. In this respect, the data presented here further strengthen the links that are increasingly being drawn between mechanisms that underpin basic visual sensory processing and those which are involved in the short term retention of this information (Pasternak & Greenlee, 2005).

Results from contrast adaptation experiments have made fundamental contributions to the elucidation of the organisation of low-level sensory processing of spatial frequency information in the primate visual system (Bjorklund & Magnussen, 1981; Blakemore & Campbell, 1969a, 1969b; Georgeson & Harris, 1984). Nonetheless, whilst perceptual memory mechanisms appear to share common properties with basic sensory processing, it is important to note that there are differences between results that have emerged from contrast adaptation and memory masking experiments. These

may serve to highlight differences that exist between the neural processes that underpin sensory and memory mechanisms. For example, previous psychophysical studies have shown that the effects of contrast adaptation are greatest when the adapting and test stimuli are spatially coincident, but rapidly decrease when their separation increases (Ejima & Takahashi, 1984, 1985; Williams et al., 1982). Memory masking for spatial frequency, on the other hand, still occurs for effective mask stimuli, with little decrease in magnitude, at horizontal separations of up to 6°, distance well outside that measured for contrast adaptation effects (Ejima & Takahashi, 1984). These long range effects are at odds with single-unit neurophysiological experiments which have shown, albeit for very different complex motion stimuli, that the short term retention of visual information is highly spatially localised (Zaksas et al., 2001). However, they are consistent with other psychophysical results (Tanaka & Sagi, 1998a), which demonstrated the existence of spatially long range and long lasting facilitation effects in the detection of Gabor contrast patterns. This study highlights the fact that low-level spatial filters do have the capability to retain information about visually presented patterns far beyond their normal limits of spatial and temporal integration and may form the basis for the storage of spatial information in memory (Tanaka & Sagi, 1998a, 1998b). Nonetheless, the fact that the effects mediated by perceptual memory mechanisms appear to have a much broader range of transfer across space and orientation compared to those mediated directly by low-level sensory mechanisms, suggests they are likely to be supported by neural processing at a level beyond V1 where neurons have the ability to integrate across different stimulus attributes (De Valois & De Valois, 1988). In this respect the effects of memory masking are similar to those exhibited by complex after-effects, such as the gender specific face after-effect

which are considered to be mediated by high level visual areas (Afraz & Cavanagh, 2009). Furthermore, the fact that memory masking has been shown to be dependent upon distal as opposed to retinal spatial frequency (Bennett & Cortese, 1996) also argues that perceptual memory operates at a level beyond V1 where size and shape constancies are computed.

In summary, in this study we have employed a delayed spatial frequency discrimination task in conjunction with a memory masking paradigm. We measured the changes in PSE values as a result of mask stimuli of various spatial frequencies. We have found spatial frequency dependent, selective masking effects that had bandwidths that were comparable to the bandwidths of spatial frequency channels in sensory processing. Apart from the similarities between these mechanisms we have found important differences as well, for example, the memory masking effect was independent of spatial location which might serve as evidence for the involvement of higher order cortical areas in perceptual memory mechanisms.

6.3 The Effect of Mask Contrast

6.3.1 Introduction

Adaptation experiments have made a major contribution to our present knowledge about the organisation of sensory information in vision. These experiments found evidence for increased contrast detection thresholds when observers adapted to gratings of higher contrast and of similar spatial frequencies (Blakemore & Campbell, 1969a; Blakemore et al., 1970; Greenlee et al., 1991a). At any contrast levels, the interference effect is minimal when the spatial frequency of the adaptor and the matched grating are equal. In the case

when the adaptor has lower spatial frequency than the test, it is perceived as being of higher spatial frequency, whereas if the adaptor has higher spatial frequency than the test, the mismatch is made at lower spatial frequency levels. Even though changing contrast levels do not alter this specific pattern, it has been shown that increasing adapting contrast levels result in greater perceived shifts (i.e. greater mismatch or detection threshold) within the effective adaptor spatial range (i.e. spatial frequency and orientation) (Blakemore et al., 1970). This could be explained by changes in the sensitivity of the individual spatial frequency channels due to adaptation to different contrast levels. Both the contrast detection threshold elevation and the 'mismatch' effect have similar bandwidths of 1.5 octaves. The effect diminishes 1.5 - 2 octaves away from the spatial frequency of the adaptor on the high and low spatial frequency side, respectively (Blakemore & Campbell, 1969a; Blakemore et al., 1970). This experiment provided further evidence in favour for the existence of multiple spatial frequency channels and might also indicate some degree of interaction between contrast and spatial frequency information at the early processing stages of vision.

Greenlee and Georgeson (Greenlee et al., 1991a) also examined adaptation effects of gratings of different contrast levels - among other different factors in adaptation, such as adapting time, effect of spatial frequency, and retinal eccentricity - and similarly found that as the contrast of the adaptor increased, the contrast detection thresholds rose as well (Blakemore & Campbell, 1969a; Blakemore et al., 1970).

Contrast has also been found to affect the spatial frequency discrimination ability for gratings in simple, simultaneous matching experiments, where

discrimination thresholds were found to be higher at lower contrast levels. The performance did not further decrease when they introduced time delay for up to 30 s (Magnussen et al., 1990). Overall, this indicates that it is more likely that the contrast levels interfere with spatial frequency discrimination at the sensory processing stage and not in memory (Magnussen et al., 1990).

Results from dual-task experiments have also provided evidence in support of the idea of separate storage mechanisms for spatial frequency and contrast information in VSTM (Magnussen et al., 1996). In such tasks, observers were required to retain information about the contrast level and spatial frequency of luminance gratings. Both the spatial frequency and the contrast of the grating were varied, and observers had to make judgments about both stimulus attributes simultaneously. They found elevated thresholds owing to a stimulus uncertainty effect, and when this effect was discounted, the simultaneous introduction of changes in spatial frequency and contrast did not result in higher discrimination thresholds. This supports the theory of separate processing of spatial frequency and contrast information in VSTM (Greenlee & Thomas, 1993; Magnussen et al., 1996).

We employed a memory masking paradigm with the aim to investigate whether increasing mask contrast levels induce increasing perceived spatial frequency changes in VSTM. We expected the higher contrast stimuli to have a stronger effect on the memory induced shifts whereas masks of lower contrast should result in smaller shifts in the PSE. In all cases we expected the PSE values to vary in a characteristic manner as seen in the previous experiments as a function of mask spatial frequency.

6.3.2 Methods

The reference had a spatial frequency of 1 c/deg, and test spatial frequencies fell within a range of 0.91 - 1.09 c/deg in seven equal steps as before. Reference and test contrasts were set to a 50% level. Achromatic masks within a range of 0.5 - 6 c/deg at three different contrast levels were employed (10, 50, 100 %) in the different runs. Reference, test and mask stimuli were presented in a spatially separated fashion, the reference appeared on the right, the test on the left of the central fixation mark and the mask was presented in the centre of the screen without any spatial overlap between the stimuli (**Figure 6.1**). An ISI of 5 s was employed, the mask appeared in the middle of the time delay for 2 s. Two observers completed these experiments (VN, DM).

6.3.3 Results

Data was plotted as a function of mask spatial frequency for the different contrast levels (**Figure 6.12**). Examining the PSE values, the same characteristic tuning emerged at all three contrast levels.

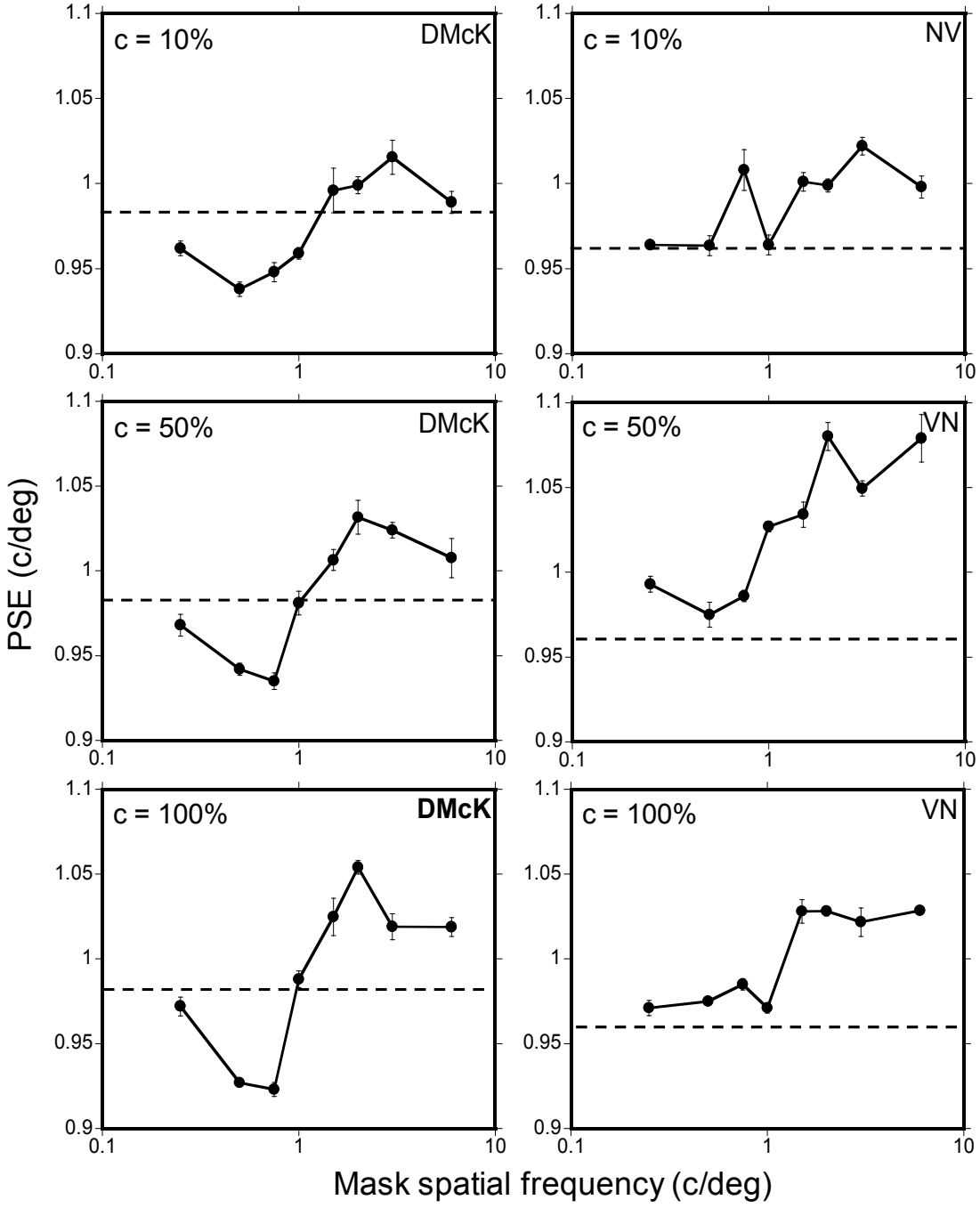


Figure 6.12 The effect of mask contrast. PSE values were plotted as a function of mask spatial frequency on a logarithmic scale. Three mask contrast levels were employed, 10, 50, 100%. Data from two observers (DM, VN). Error bars indicate errors of the logistic curve fits.

The values of the two observers were averaged and plotted on **Figure 6.13** in order to examine whether there is any difference in the PSE values at the different contrast levels. It is apparent from the data that although the shape of the characteristic tuning effects are the same for all three mask contrast levels,

the different levels cause considerably different amounts of shifts in the PSE and discrimination threshold values.

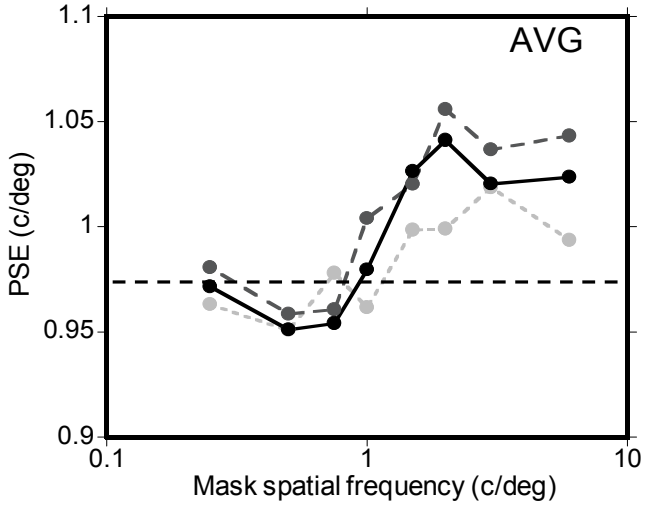


Figure 6.13 The effect of mask contrast. Averaged PSE data replotted from **Figure 6.12**. Light grey data points (connected by dashed line) correspond to 10%, dark grey (connected by dashed line) to 50% and data points (connected by solid line) represent 100 % contrast levels.

In order to investigate the magnitude of this effect and compare differences, the averaged data were fitted with the first derivative of the Gaussian function and presented in **Figure 6.14.** This curve fit, apart from giving an estimate of a function, gives a measure of the amplitude of the effects, i.e. the greatest PSE values. The amplitude in this case is the half height of the curves and the values are plotted on **Figure 6.15** (for details on these measures and the curve fitting procedure see **Chapter 3**, **Section 3.7.2.3**). The amplitude values represent the magnitude of the PSEs, and are expressed in c/deg. The amplitude values show an increase with increasing mask contrast, and this effect saturates at high contrast values as indicated by the fitted Naka-Rushton function on **Figure 6.15** (Nelson & Takahashi, 1999). This finding is in agreement with previous contrast adaptation studies (Blakemore & Campbell, 1969b; Blakemore et al., 1970).

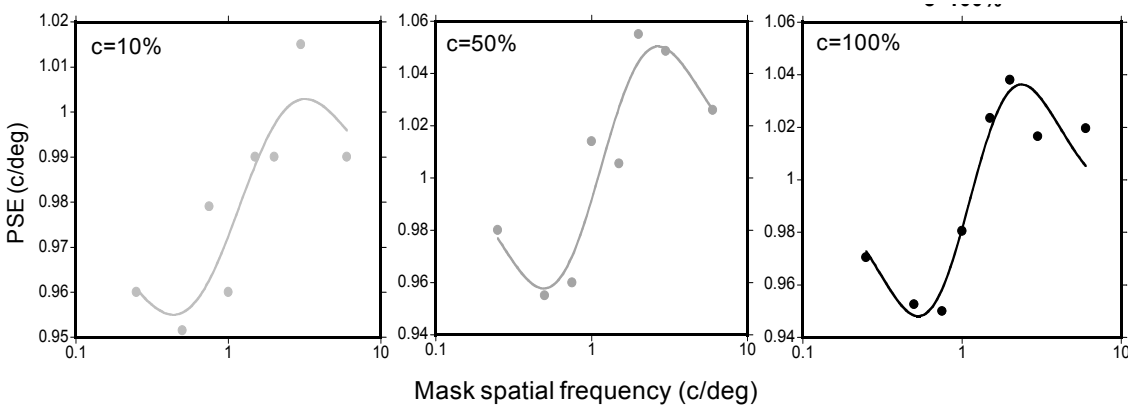


Figure 6.14 The effect of mask contrast. Averaged PSE data replotted from Figure 6.13 and fitted with the 1st derivative of the Gaussian function. As indicated on the individual curve fits, light grey data points correspond to 10%, dark grey to 50% and black data points represent 100 % contrast levels.

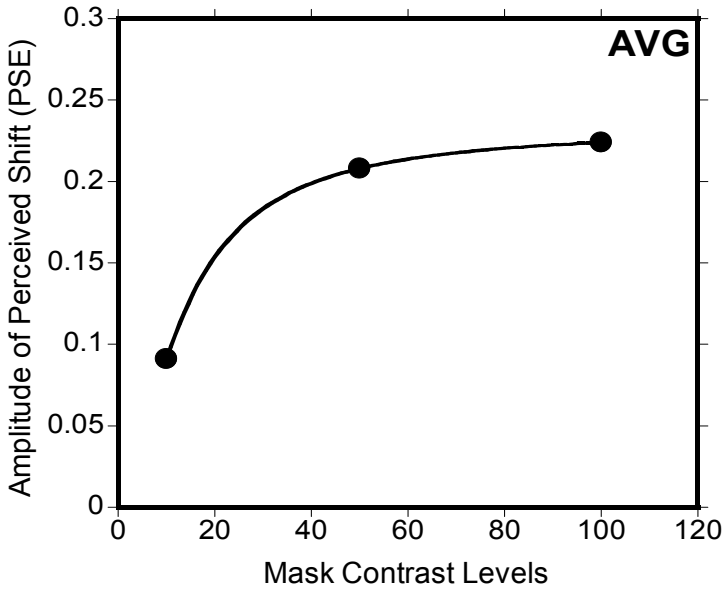


Figure 6.15 The effect of mask contrast. Amplitude values in case of the different mask luminance grating contrast levels taken from the curve fitting results represented on **Figure 6.14**. The data is fitted with the Naka-Rushton formula in order to indicate the saturating nature of the contrast effect (Nelson & Takahashi, 1999).

6.3.4 Discussion

Our main finding, that there is a change in PSE values as a result of contrast changes, i.e. higher contrasts result in greater PSE shifts, and as a function of spatial frequency is in agreement with contrast adaptation experiments (Blakemore et al., 1970). Changes in the contrast level of the mask stimulus seem to have an influence on the memory masking effect. There is a tendency

of higher contrast values to cause a greater shift in the stored representation of the spatial frequency of the reference (Blakemore et al., 1970). This finding is in agreement with previous results, stating that higher contrast levels result in greater shifts in PSE (Blakemore & Campbell, 1969a; Blakemore et al., 1970; Lee & Harris, 1996) and indicates that interference occurs between contrast and spatial frequency mechanisms in visual perceptual memory. This might mirror the fact that in visual perceptual memory the memory and sensory processing mechanisms are closely allied and might be served by similar cortical areas (Bisley & Pasternak, 2000; Fuster, 1997; Graham et al., 2010; Pasternak & Greenlee, 2005).

It has also been shown, that the representation of contrast becomes less accurate in memory, which, according to Lee and Harris (Lee & Harris, 1996) could be due to three different mechanisms, such as deterioration of the representation (i.e. contrast decreases in memory), convergence of all remembered contrast levels to an average value, or the stored contrast level remains constant but the representation becomes noisy (Lee & Harris, 1996). Their data did not show fading and nor did they find evidence in favour of the idea that the memory representation converges to a central value. Moreover they found that there is one single storage mechanism that is involved in contrast change detection during the first 10 s of memory. The pattern of decay or visual forgetting for contrast memory was similar at all spatial frequencies (Lee & Harris, 1996).

In the experiment of Greenlee and Thomas (Greenlee & Thomas, 1993), in single and dual judgment tasks, observers judged either the spatial frequency, or the remembered contrast of the gratings. They found that once the

uncertainty effect was discounted, it was apparent that the dual task did not result in elevated thresholds, which confirmed the theory according to which there are separate processing channels for contrast and spatial frequency. They formed an uncertainty model that assumes that spatial frequency and contrast are processed separately, at the level of VSTM. This finding contradicts our results that were drawn from memory masking experiments and are more along the lines of the contrast adaptation ones (Blakemore & Campbell, 1969b; Blakemore et al., 1970). One possible explanation would be that a memory masking paradigm exploits different mechanisms as compared to dual judgment tasks.

In summary, we have found stimulus specific mechanisms for contrast in perceptual short term memory for spatial frequency in agreement with earlier studies (Lee et al., 1996). Increasing mask contract levels had an increasing effect on the PSE changes in a pattern which shows similarities with the results of contrast adaptation experiments (Blakemore et al., 1970). Higher contrast values resulted in higher PSE values. This result suggests that there might be an interconnected processing mechanism for contrast and spatial frequency information in VSTM.

6.4 The Effect of Orientation

6.4.1 Introduction

In these experiments we aimed to investigate the organisation of orientation information in VSTM in view of the results of previous contrast adaptation experiments. We were also looking for evidence in favour of the separate, dimension specific information processing in VSTM.

Experiments have shown that increases in contrast detection thresholds that occur after adaptation to high contrast gratings are orientation specific (Blakemore & Nachmias, 1971). However, this effect only takes place within a narrow orientation range (±40°) and when the difference in orientation between the adaptor and test grating exceeds this range, the adaptation phenomenon disappears (Blakemore et al., 1970). Blakemore and Nachmias (1971) also found similar orientation selectivity for the adaptor specific shift in the perceived spatial frequency. These findings imply that the sensory adaptation to spatial frequency and orientation and the resulting increase in discrimination thresholds and perceived spatial frequency shifts take place at a common site in the visual system, probably at the level of visual cortex (Blakemore & Nachmias, 1971).

In these experiments we intended to use the memory masking paradigm to investigate whether induced PSE shifts in the remembered spatial frequency are also tuned for orientation. Earlier studies have shown that masking stimuli of different orientation did not result in elevated discrimination thresholds in a delayed match-to-sample paradigm (Magnussen et al., 1991), which demonstrates that memory masking occurs in case of relevant stimulus dimensions only (Magnussen & Greenlee, 1999). In these experiments, we expected that changing the orientation of the mask in a delayed spatial frequency matching experiment, would have no effect on performance, as indicated by invariant PSEs values.

6.4.2 Methods

Reference had a spatial frequency of 3 c/deg, and test spatial frequencies ranged within 2.55 - 3.45 c/deg in seven equal steps. Reference and test contrasts were set to a 50% level. Achromatic masks of 1.5, 3 and 6 c/deg were

presented in different orientations (90°, 112.5°, 135°, 157.5°, 180°) in separate trials. Two observers completed these experiments (VN, DM), and one additional observer carried out runs for orientations of 90°, 135° and 180°. Reference, test and mask stimuli were presented in a spatially separated fashion, as explained in **Section 6.2**; the reference appeared on the right, the test on the left of the central fixation mark and the mask was presented in the centre of the screen without any spatial overlap between the stimuli, along a horizontal axis. An ISI of 5 s was employed, during which the mask appeared in the centre of the delay for 2 s. The paradigm is explained in detail in **Section 6.2.2**.

6.4.3 Results

Figure 6.16 shows the data from these experiments. It is apparent from the data that the orientation of the mask grating in a delayed spatial frequency discrimination experiment has no major effect on the PSE values (**Figure 6.16**). The perceived shift of the test grating is invariant in case of similar luminance grating mask spatial frequencies, regardless of their orientation. The effective masks (1.5 and 6 c/deg) induce similar shifts above and below baseline, irrespective of the orientation, and likewise, ineffective mask stimuli (i.e. when spatial frequency is the same as of the reference) do not result in shifts in the perceived spatial frequency at any of the mask grating orientations. In other words, the effect of the mask grating is independent of its orientation, which indicates that spatial frequency and orientation do not interact in VSTM.

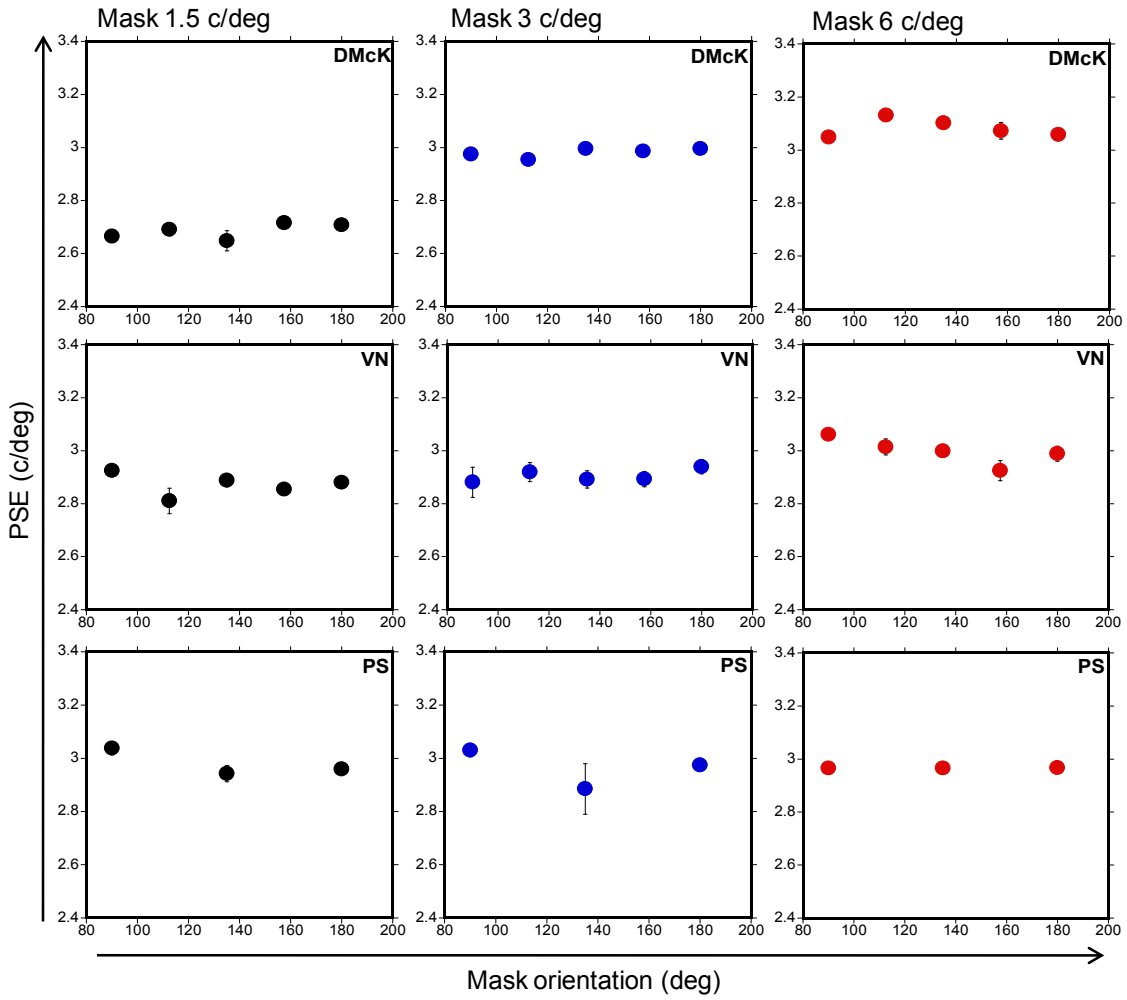


Figure 6.16 The effect of mask orientation. PSE values were plotted as a function of mask orientation (expressed in degrees). Each row represents data from an individual observer and columns show data for masks of 1.5, 3 and 6 c/deg. Error bars indicate errors of the fits.

6.4.4 Discussion

In this experiment we investigated the interaction between spatial frequency and orientation in VSTM. We have found evidence that the retention of spatial frequency information lacks orientation selectivity, since very different grating orientations failed to alter the memory masking effects that were present at similar orientations (Regan, 1985). It has been known that there are common mechanisms that basic sensory processing and perceptual memory share. However there are also differences between the results of contrast adaptation and memory masking experiments, which might point to the existence of

differences between these mechanisms. One of these differences has been shown in the processing of orientation information, namely, that the retention of spatial frequency information in perceptual memory lacks orientation selectivity (Regan, 1985). For perceptual memory mechanisms, an effective masking stimulus remains effective regardless of its orientation (Magnussen et al., 1996). Contrast adaptation experiments contributed to our present understanding of the organisation of low-level sensory processing of spatial frequency information to a great extent (Bjorklund & Magnussen, 1981; Blakemore & Campbell, 1969a, 1969b; Georgeson & Harris, 1984). In low-level sensory processing, the spatial frequency and orientation information seems to be interconnected (Blakemore & Nachmias, 1971; Blakemore et al., 1970), i.e. the effects of adaptation to a luminance contrast grating are highly orientation dependent and are abolished if the adapting and test grating differ by more than 40° (Blakemore & Campbell, 1969a, 1969b; Blakemore & Nachmias, 1971; Blakemore et al., 1970; Movshon & Blakemore, 1973). This is in stark comparison to perceptual memory experiments (Blakemore & Nachmias, 1971; Blakemore et al., 1970; Magnussen et al., 1996; Regan, 1985).

Neuroimaging studies also found that when observers had to retain information about spatial frequency in VSTM as the orientation of the gratings was varied, most of the increased activation took place in sensory areas (V1 and V2) (Baumann et al., 2008). The accuracy was invariant in the different conditions, but when an additional stimulus dimension was introduced there was a rise in the reaction times when the gratings were orthogonal, which on the contrary might imply that they are not separately processed. The activation of V1 and V2 were in close correlation with the changes in reaction times, possibly meaning that these areas take part in the sensory processing of these stimuli. However,

prefrontal and parietal cortical activation does not change at all when an irrelevant stimulus dimension is introduced. Harrison and Tong found similar results with a pattern analysis technique, that the early visual areas (V1-V4) take part in the maintenance of visual information in VSTM (Harrison & Tong, 2009). In this experiment, memory for orientation was examined in a delayed match to sample task while they monitored brain activation with fMRI. Moreover, V1 and V2 showed a pattern specific activation depending on the orientation of the grating that had to be retained in memory (Harrison & Tong, 2009).

In summary the results of this memory masking experiment show that the retention of information in VSTM about spatial frequency is independent of its orientation. We have found evidence for important differences in the organisation of information between sensory processing and VSTM. While in case of sensory processing, contrast adaptation experiments have shown that spatial frequency and orientation information are interconnected, it seems that in VSTM the two types of information are processed independently of each other. Moreover, the effect we found is independent of retinal location, on the contrary to the spatial dependency of adaptation effects. These findings point to the involvement of long range long lasting facilitation effects in VSTM which come from higher order cortical areas beyond V1.

6.5 General Discussion

In these experiments we examined the possible similarities and links between sensory processing and VSTM with emphasis on spatial frequency. We employed a memory masking paradigm in delayed spatial frequency tasks in order to examine the fidelity of representation of this information in VSTM. We

found that stored spatial frequency information is vulnerable to disruption. Memory masks of different spatial frequencies were able to shift the stored representation of spatial frequency. This effect had a bandwidth of 1.2 octaves. This finding highlights the existence of multiple, spatially tuned mechanisms in visual perceptual memory, which mirrors the organisation of information in sensory processing (Magnussen, 2000, 2009; Magnussen & Greenlee, 1999). Moreover, the above findings were independent of retinal location which implies that there is and involvement of higher order cortical mechanisms in VSTM.

Increasing differences in contrast of the memory masking stimuli seem to enhance this effect, resulting in greater PSE changes while the pattern of the memory masking effect remains unaltered. This finding is similar to what has been found in contrast adaptation experiments (Blakemore & Campbell, 1969b; Blakemore et al., 1970). On the other hand, we have also shown that changing the orientation of masking stimuli does not reduce the ability of effective memory masking stimuli to induce shifts in the PSEs. This implies that spatial frequency and orientation are likely to be processed separately in VSTM, a finding which suggests a difference with sensory processing where these two attributes are closely combined.

A characteristic property of visual information that is retained within low-level perceptual memory highlighted by this and other studies is that it is malleable and vulnerable to interference (Magnussen, 2009). This suggests that there may be some overlap with a weak or fragile form of visual short term memory (VSTM), the existence of which has been questioned by certain studies (e.g. (Sligte et al., 2008, 2009)). These studies form part of a wider body of work which describes the transfer of low-level sensory information into memory as a

multi-stage process (Lalonde & Chaudhuri, 2002; Magnussen et al., 1998; Sligte et al., 2008, 2009; Tanaka & Sagi, 2000). Within this process, the weak form of VSTM operates for temporal durations of the order of 4 s or less (Lalonde & Chaudhuri, 2002; Magnussen et al., 1998), is closely allied to low-level sensory processing and is vulnerable to interference. Currently, it is an open question as to whether weak VSTM actually forms part of a continuum with iconic visual memory, or is in fact a distinct and separate process in itself (Sligte et al., 2009). However, regardless of this issue the properties of weak VSTM do have much in common with the characteristics of low-level perceptual memory as revealed in this study and in all likelihood are similar mechanisms. For longer durations, a stronger form of VSTM is proposed to exist which is characterised as having a limited storage capacity and is less vulnerable to interference (Sligte et al., 2008, 2009; Vogel et al., 2006). A key feature which further differentiates it from the weak form of VSTM is the fact that strong VSTM appears to be under the control of attention which gates low-level visual signals as part of the generation of more long term memory representations (Lalonde & Chaudhuri, 2002; Tanaka & Sagi, 2000). Recent brain imaging studies have shown that the neural activity that accompanies VSTM is distinct from that which accompanies attention lies outside of the early visual areas (Offen et al., 2009) and that the level of activation of area V4, in particular, may provide an index as to strength of the representation in VSTM (Sligte et al., 2009).

By employing stimuli that were spatially separated, we have also shown that the interference caused by memory mask stimuli have a much broader spatial extent across retinal locations. Contrast adaptation typically takes place within coincident retinal locations and decreases with spatial separation, whereas our stimulus configuration allowed us to examine interference between stimuli that

were spatially non-coincident. The results indicate that there is probably an involvement of higher order areas in VSTM where the processing of information is not dependent on retinal location. This finding contradicts previous ones that showed spatial dependence of memory masking effects in VSTM (Zaksas et al., 2001), but these experiments employed very different stimuli. Some other studies, however, suggest that spatial information is computed across retinal locations (Ester et al., 2009), as well as results from Tanaka and Sagi, who showed longer range and long lasting facilitatory effects in case of the contrast grating detection mechanisms (Tanaka & Sagi, 1998a, 1998b). This organisational principle might serve as a basis for VSTM and highlights the possibility of the involvement of neural processing that takes place beyond V1, at a level where neurons are capable of integrating information across different stimulus attributes.

In conclusion, the experiments in this chapter demonstrate that the mechanisms that underpin the short term retention of information about spatial frequency in perceptual memory are tuned in similar manner to the channels or filters that operate right from the earliest levels of low-level spatial processing. This further emphasises the link between memory mechanisms and basic sensory processing mechanisms that are being used as a basis for the retention of information. However, whilst certain characteristics of perceptual memory are highly consistent with the kind of analysis that occurs in the earliest stages of visual processing, the broad transfer properties of memory masking across location and orientation for example, suggest more complex interactions. Such interactions are likely to involve visual areas beyond the primary visual cortex. In this and other respects low-level perceptual memory shares common properties with the weaker form of VSTM that have been described previously.

Chapter 7

Investigation of Perceptual Short Term Memory for Motion

7.1 Introduction

7.1.1 Cortical Substrates of Motion

The perception of visual motion involves the analysis of speed and direction of moving components of a visual scene. Motion processing in the human cortex mainly takes place via an anatomically separated pathway, the magnocellular system (Hawken et al., 1988). This pathway projects to layers 4Cα and 4B of V1 via the magnocellular layers of the LGN (Hubel & Livingstone, 1990). In V1, there are cells selective for the direction of motion of an image feature, each cell responds selectively to its specific favoured direction of contour that falls within its receptive field and they transfer this information to MT/V5 (Van Essen & Gallant, 1994). These cells constitute approximately 30% of the total neuron population in V1 (Hubel & Wiesel, 1968). From V1, the pathway carries on to V5/MT via the dorsal processing stream. Area V5/MT in the temporal lobe carries out the second stage of motion analysis. It is considered to be the centre of higher order visual motion processing in monkeys and humans (Dubner &

Zeki, 1971; Livingstone & Hubel, 1988; Maunsell & van Essen, 1983; Tootell et al., 1995b; Zeki, 1978). V5/MT receives most of its afferent connections from V1 (Movshon & Newsome, 1996), via the thick stripes of V2 (Anderson & Martin, 2002) and from area V3 (**Figure 1.12**) (Gegenfurtner et al., 1997). A substantial proportion of the cells in V5/MT are selective for the direction of motion (Maunsell & van Essen, 1983) and speed instead of the spatial or temporal frequency content of the stimulus (Perrone & Thiele, 2001). Among areas that encode specific, complex types of motion is V3A, which is believed to take part in the processing of coherent motion (Tootell et al., 1997), the Kinetic Occipital (KO) area has a role in analysing contours that are defined by differences in velocity (Zeki et al., 2003) and the Superior Temporal Sulcus (STS) which processes biological motion (Thompson et al., 2005).

Neuroimaging studies using fMRI showed elevated BOLD signal in V1 and area V5/MT in response to moving stimuli. Counter-phase flickering gratings, pattern motion stimuli, moving chromatic stimuli and motion after effects evoked a stronger activation in V5/MT as opposed to V1, indicating that these stimuli utilized higher forms of motion encoding mechanisms (Ffytche et al., 1995a; Heeger et al., 1999; Huk et al., 2001; Tootell et al., 1995a; Wandell et al., 1999). Induced transient lesion studies employing TMS also showed that MT/V5 is responsible for the analysis of motion, motion discrimination, speed discrimination and coherent motion (Matthews et al., 2001; Rudolph & Pasternak, 1999).

7.1.2 Motion Perception

Motion perception can be achieved in several ways depending on stimulus properties; high contrast chromatic stimuli are processed via low level motion

detectors, whereas low contrast chromatic stimuli are processed by higher order cognitive mechanisms (e.g. position tracking) (Cropper & Derrington, 1994, 1996; Seiffert & Cavanagh, 1999). Low level motion processing involves the immediate analysis of spatiotemporal position (i.e. image displacement detection), whereas high level motion processing involves a consecutive analysis of the seen information in a timely order (i.e. integration of motion information taking the object origin into account). In terms of the structure of the stimulus, there exists first-order motion perception, which exploits luminance differences and is probably perceived by velocity sensitive motion energy mechanisms, whereas second-order motion is defined by texture or binocular disparity-luminance variance, analysed by a position sensitive detector (Cropper & Wuerger, 2005). Low contrast or slowly moving equiluminant chromatic (red-green) gratings are detected by position tracking, whereas high contrast or high speed equiluminant chromatic stimuli (or texture based) are analysed by the velocity sensitive (motion energy) mechanisms (Cropper & Wuerger, 2005). Both systems take part in the perception of motion of second order stimuli and their relative participation depends on the contrast and speed of the stimulus (Cropper & Wuerger, 2005; Seiffert & Cavanagh, 1999).

The perceived speed of a stimulus depends on numerous stimulus parameters such as contrast (Stone & Thompson, 1992); stimuli of higher contrast are perceived as moving faster, whereas patterns of lower contrast appear to move slower (Hawken et al., 1994). Perceived speed for colour and luminance defined stimuli are also different, there is an apparent reduction in the speed of coloured stimuli, which implies that motion information defined by colour and luminance are analysed via separate pathways on the basis of colour and luminance (Cropper & Wuerger, 2005; Hawken et al., 1994). This holds

especially for stimuli that move slowly (Chatterjee & Callaway, 2003; Cropper & Wuerger, 2005; Gegenfurtner et al., 1994).

7.1.3 Colour and Motion

In monkeys and humans, the motion of visual stimuli that is signalled by spatiotemporal changes in luminance is generally thought to be processed by the magnocellular pathway. The most important cortical location in this pathway is MT/V5 (Livingstone & Hubel, 1988; Tootell et al., 1995a; Zeki, 1978). The magnocellular system has low sensitivity to the wavelength composition of the stimulus, therefore it has been suggested that the processing of colour defined motion is carried out by a different mechanism, the parvocellular pathway (Schiller & Logothetis, 1990).

There are currently conflicting views as to the extent of segregation between the processing of colour and luminance defined motion, and in particular the extent to which the chromatic properties of a moving stimulus are utilized in its motion analysis (Cropper & Wuerger, 2005; McKeefry et al., 2006). According to traditional views, luminance and colour information are separately processed in the visual system in different anatomical pathways (Livingstone & Hubel, 1988; Livingstone & Hubel, 1987; Ramachandran & Gregory, 1978; Zeki, 1978). According to this notion, motion analysis largely relies on spatiotemporal modulations in luminance without exploiting the chromatic signal. This poses the question whether chromatic motion is processed by the motion system or by the mechanisms that are devoted to the analysis of colour or both, depending on the stimuli.

While studies in favour of the segregated processing theory advocate that chromatic and luminance motion processing takes place in anatomically distinct

channels, others revealed interactions between the two mechanisms (Krauskopf & Farell, 1990; Willis & Anderson, 1998). Neurophysiological studies support the idea that there is no clear separation between these pathways, and that colour and luminance motion processing share a common mechanism (Barberini et al., 2005; Cavanagh & Anstis, 1991; Cavanagh & Favreau, 1985; Dougherty et al., 1999; Seidemann et al., 1999; Wandell et al., 1999). According to recent evidence, colour contributes to chromatic motion perception (Cavanagh et al., 1984; Cropper & Derrington, 1996; Cropper & Wuerger, 2005; Dobkins & Albright, 1994; Dougherty et al., 1999; Gegenfurtner et al., 1994; Seidemann et al., 1999), but it is still not yet known whether specialised chromatic motion detectors that are separate from luminance motion detectors are dedicated to the processing of this information. Dobkins and Albright (Dobkins & Albright, 1994) have shown that V5/MT is capable of extracting motion information at isoluminance from chromatic borders or from the sign of chromatic contrast when the former is not available.

Motion adaptation and motion after effects are other methods which have been used to examine the organisation of chromatic information in motion processing. McKeefry et al. (McKeefry et al., 2006) provided evidence to suggest that there are indeed separate channels for luminance and chromatic information in the early stages of motion processing. Furthermore, they found evidence for the existence of subdivisions for the two cone opponent cardinal mechanisms in motion analysis (Chatterjee & Callaway, 2003; Krauskopf & Farell, 1990) and that at later stages in the cortical processing hierarchy chromatic and achromatic information are integrated. According to the majority of present lines of evidence V5/MT is possibly an important cortical locus for the integration of

colour information for motion processing (Gegenfurtner et al., 1994; McKeefry et al., 2006).

7.1.4 VSTM for Motion and Speed

Psychophysical and physiological studies examining VSTM have suggested that there are parallel mechanisms in VSTM, each being responsible for the processing a particular visual dimension such as contrast, spatial frequency and speed (Bisley et al., 2004; Bisley & Pasternak, 2000; Bisley et al., 2001; Magnussen & Greenlee, 1992, 1999; Regan, 1985). Studies that have examined VSTM for motion employed simple stimuli such as drifting gratings and random moving dots, in order to investigate the retention characteristics of the direction of motion as well as the speed of the stimuli. A two-alternative forced choice procedure has been traditionally employed, in which stimuli can be separated in space and in time, and the fidelity of the memory representation is assessed in terms of delayed discrimination ability and perceived subjective equality. Some of these studies employed a memory masking method, in which a third stimulus is presented during the memory delay (Magnussen & Greenlee, 1992; Magnussen et al., 1991). These memory masks induce selective effects on the delayed discrimination ability, the masks are only effective within a given stimulus parameter range, and are ineffective in the case when the reference and the mask have the same stimulus characteristics. They also observed that masks that differ in terms of an additional stimulus dimension have no additional effect on performance. Based on these results, Magnussen et al. proposed that different stimulus ranges are stored in multiple separate, individual storage mechanisms (Magnussen et al., 1996). Some of these studies also examined the location in the cortical processing stream where interactions might take

place between the different stimulus dimensions for the retention of speed (Magnussen & Greenlee, 1992). The interaction during the masking phenomena possibly occurs at higher levels, as it is only the speed that causes disruption of the fidelity of information while the direction of motion has no effect, implying that they are separately processed at this level of interaction (Magnussen & Greenlee, 1992).

Magnussen and Greenlee (Magnussen & Greenlee, 1992) have shown that the ability to retain information about stimulus speed in VSTM is highly accurate for time delays of up to 30 s. As in studies for other stimulus dimensions, the accuracy of the stored information can be disrupted by a masking stimulus that is presented during the memory interval. It has also been found that discrimination threshold values for speed show minimal change when the mask speed corresponds with the speed of the reference but different mask velocities (either lower or higher) result in increased values (Magnussen & Greenlee, 1992). This memory masking effect, while observers retain information about the speed of a moving grating, is independent of the direction of motion, which might imply that the direction of motion and speed are processed separately in VSTM.

McKeefry et al. (McKeefry et al., 2007) examined the speed selectivity of VSTM employing a memory masking paradigm in a delayed match-to-sample task. The aim was to examine whether VSTM for speed is selective for the spatiotemporal characteristics of the stimuli, which is more representative of V1 (Adelson & Movshon, 1982), or whether it is more selective for the speed, independent of the spatial or temporal frequency of the stimulus, which would imply the major role of MT/V5 in the process (Perrone & Thiele, 2001). By changing the spatiotemporal composition of the mask they found that minimal

masking occurred in cases when the reference and the mask had the same speed, independent of the spatial and temporal frequency composition of the stimulus, which confirms selectivity for speed in VSTM and highlights the possible central role of V5/MT.

Experiments examining VSTM for the direction of motion for random dot stimuli also confirmed a high accuracy in VSTM for delays up to 6 s (Bisley & Pasternak, 2000; Bisley et al., 2001; Zaksas et al., 2001). Moreover they found that the effect of the memory mask stimulus is location selective (Zaksas et al., 2001), the mask was only effective in the case when it appeared in the same location as the test and discrimination thresholds increased beyond a certain degree of spatial separation. This is a finding which they concluded to support the notion that the areas involved in VSTM are retinotopically organised.

7.2 The Effect of Mask Velocity for Chromatic and Achromatic Masks

7.2.1 Introduction

As explained in **Section 7.1** it is still a matter of debate to what extent colour information is exploited in the processing of motion (Cropper & Wuerger, 2005). We aimed to examine speed selectivity in VSTM as well as to what extent colour and luminance information are processed separately in VSTM for motion. In order to do this, we examined the effect of moving mask stimuli of a range of speed values. The mask sinusoidal gratings were either generated by luminance contrast or chromatic contrast in order to examine the degree to which these different types of mask stimuli were able to disrupt the precision of the representation of the moving stimulus in VSTM.

In this study we wished to explore the degree to which information about different stimulus dimensions are segregated in terms of their storage in VSTM for the speed of motion. In order to investigate this issue, we employed a memory masking paradigm that exploits the phenomenon that the perceived speed of a stimulus can be modified by another stimulus, which has similar velocity (Magnussen & Greenlee, 1992; Smith & Derrington, 1996). We hypothesised that in case VSTM for velocity is organised via parallel channels, the mask induced perceived speed shift will show specific patterns as demonstrated in previous chapters (**Chapters 5** and **6**). Memory masking should be marked in case of similar velocities and minimal at identical velocities and when the velocity of the mask is substantially different from that of the reference.

We were also interested in the effect of chromatic content on the retention of speed information in VSTM. We were specifically interested in exploring whether the chromaticity of the masking stimuli influenced its ability to interfere with the stored representations of luminance contrast gratings. We assumed, that if the visual system was able to exploit chromatic information for the analysis of speed, same way as in case of luminance, then the characteristics of discrimination threshold and PSE changes as a result of memory masking would be exactly the same in all cases.

7.2.2 Methods

Stimuli consisted of vertically oriented drifting sinusoidal luminance gratings, which moved with a range of velocities and were presented on a colour graphics monitor (GDM; Sony, Tokyo, Japan; frame rate 120 Hz) and controlled via a video graphics card (VSG 2/5; Cambridge Research Systems, Rochester,

UK). The gratings appeared in a square window of 2.5° x 2.5° in the centre of the screen on an equiluminant grey background (illuminant C = 12.5 cd/m^2, CIE coordinates: x = 0.310, y = 0.316). Mask stimuli were vertically oriented moving sinusoidal luminance or chromatic gratings that had a spatial frequency of 1 c/deg and velocities spanned within a range of 0.75 and 24 deg/s. The hues of the masking stimuli represented the 0° - 180° axis of modulation in MBDKL colour space (Derrington et al., 1984), in which changes along the azimuth (ϕ) modulate the chromatic content of the stimuli on the isoluminant plane, whereas changes in elevation (θ), modulate the luminance contrast. θ = 0° defines isoluminant and ($\theta = \pm 90°$) characterizes luminance gratings (McKeefry et al., 2006). The luminance ratio of the luminance gratings was set to 1 (θ = +90°), in case of the mask chromatic gratings it was equal to 0.5 (see **Section 3.3.2)**, and contrast level was set to 50%.

The spatial frequency of the reference was 1 c/deg, the temporal frequency was either 3 or 6 c/s (Hz) and therefore velocities of the reference stimuli were 3 and 6 deg/s, respectively (see **Chapter 3**, **Section 3.4**). The test stimuli corresponded with seven velocities within a range of $\pm$ 40% (between 4.5-7.5 deg/s) of the reference, in steps of 0.5 deg/s for one observer (DMcK) and between 3.75 and 8.25 for the other observer (VN) in steps of 0.75 deg/s. These step sizes were adjusted to the discrimination ability of the individual in order to yield a high level of accuracy at either end of the test velocity spectrum and a gradual slope to 50% accuracy in the middle range of the test velocities. The contrast was set to 50% for all stimuli, and varied randomly across $\pm$ 5% to prevent the build-up of long term representations. The direction of the moving gratings was also varied to prevent learning. These variations were balanced over the trials in order to minimise any bias (Magnussen & Greenlee, 1992).

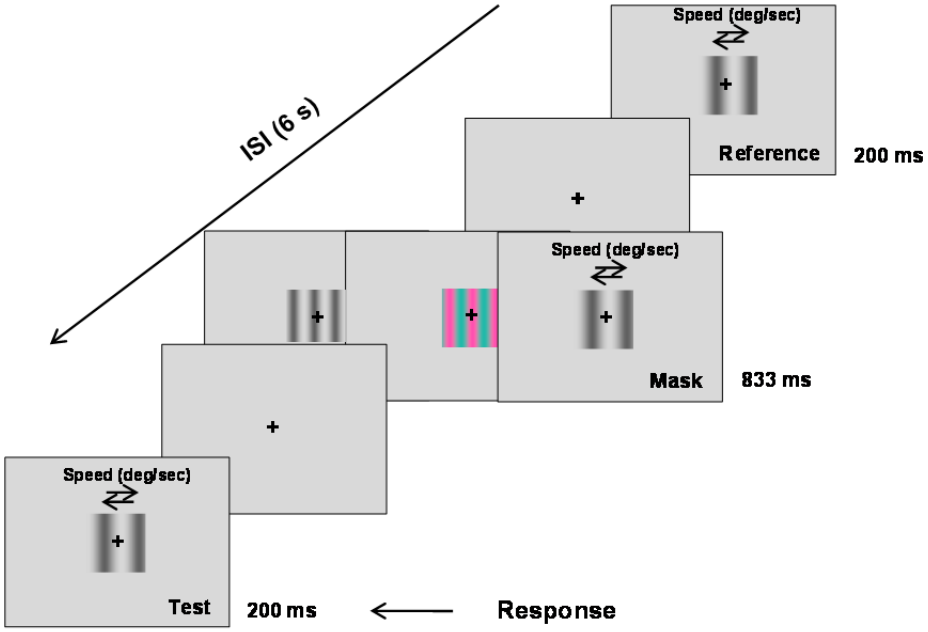


Figure 7.1 A schematic representation of the delayed velocity discrimination paradigm used in this study (exact replica of **Figure 3.22**). Each cycle began with the presentation of a reference stimulus (3 or 6 deg/s) for 200 ms. Mask stimuli were presented during the 5 s long ISI for 833 ms. After the test stimuli were displayed for 200 ms, the observers were instructed to respond by a button press to indicate whether they judged the test to be of higher or lower velocity than the reference stimulus. Following the response the next presentation cycle began. The stimuli were presented at the centre of the screen while the observer kept his/her gaze on the central fixation mark.

A two-alternative forced choice procedure in conjunction with the method of constant stimuli was employed. Reference, test and mask stimuli appeared in the same position on the centre of the screen. ISI was set to 5 s (600 frames, one frame = 8.33 ms), reference and test were presented for 200 ms (25 frames), and mask appeared in the middle of the ISI at 2083 ms for a duration of 833 ms (**Figure 7.1**). Baseline values were acquired from runs where no masks were presented. As in the previous experiments, observers had to indicate whether the reference or the test grating drifted faster. Baseline performance was represented by conditions where no masking stimulus appeared during the ISI. Observers were instructed to keep their gaze on the central fixation mark and indicate whether the test stimulus was faster or slower than the reference one and communicate their answers via the response box (model CB3, Cambridge Research Systems).

Responses were plotted as '% correct answers' (i.e. % faster than reference), as a function of test velocity. As described in **Chapter 3**, **Section 3.7.2.2**, a logistic function was fitted to the matching data and the point of subjective equality (PSE, 50%) between the reference and the test stimulus was examined as well as the discrimination threshold for each condition (i.e. each mask velocity or mask duration or mask location).

Two experienced psychophysical observers took part in these experiments. Observers had normal or corrected to normal visual acuity (6/5) and normal colour vision as tested by the Farnsworth-Munsell 100 Hue test and a mean age of 38 years. Observers were positioned at a 114 cm distance and viewed the stimuli binocularly in a darkened room after 10 mins of dark adaptation.

7.2.3 Results

Speed discrimination thresholds and PSE values were determined for the reference and test employing a two-alternative forced choice procedure in conjunction with the method of constant stimuli. PSE values for the different runs are plotted as a function of mask velocity for coloured and luminance gratings (**Figures 7.2** - **7.5**). The data have been fitted with the 1st derivative of the Gaussian function (as explained in **Section 3.7.2.3**), in order to get estimates of the bandwidths of the masking effects and to compare the bandwidths of the masking effects for chromatic and achromatic mask stimuli. On the whole, most of the bandwidth values fell between 0.4 – 0.9 deg/s with no apparent difference between coloured and achromatic stimuli. Even though the data is variable, PSEs can be observed to vary in a characteristic manner relative to the baseline condition (i.e. when no mask is present). For mask velocities below that of the reference, perceived equality between reference and

test occurs at velocities that are lower than the baseline PSE. Conversely, when the mask speed is greater than the reference, PSEs are consequently greater than for the baseline condition. Mask stimuli of higher and lower speeds result in a peak and a trough of the PSE values, respectively. Even greater differences in speed result in a gradual decrease of this effect and performance returns back towards PSE values of no mask conditions (baseline). This suggests that the perceived speeds of the test stimuli are dependent on the mask stimulus velocities. Small differences in speed between the mask and the test result in marked PSE shifts towards the mask stimulus speed, these effects seem to be attractive in nature. In the case this difference exceeds a certain extent, this effect diminishes and performance returns back to baseline.

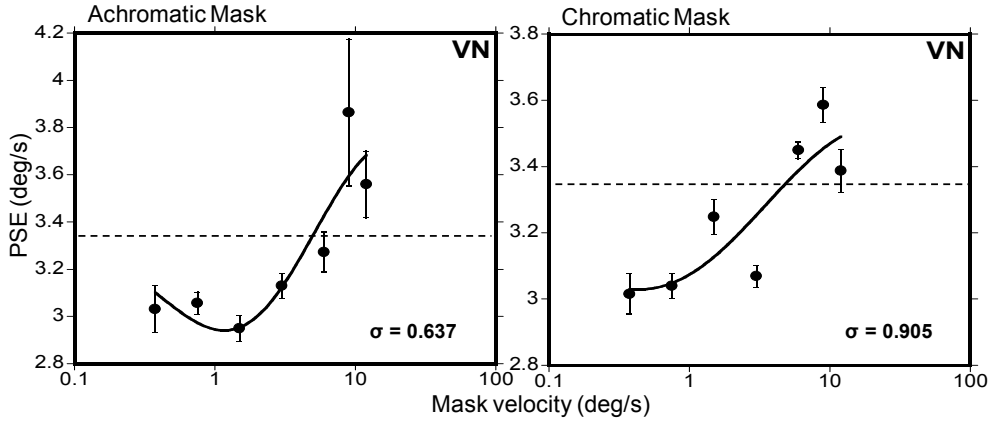


Figure 7.2 The effect of mask velocity in case of luminance and chromatic grating masks in case of a reference of 3 deg/s velocity. PSE values are plotted as a function of mask velocity. Data from one observer (VN), fitted with the 1st derivative of the Gaussian function. Error bars indicate errors of the logistic curve fits.

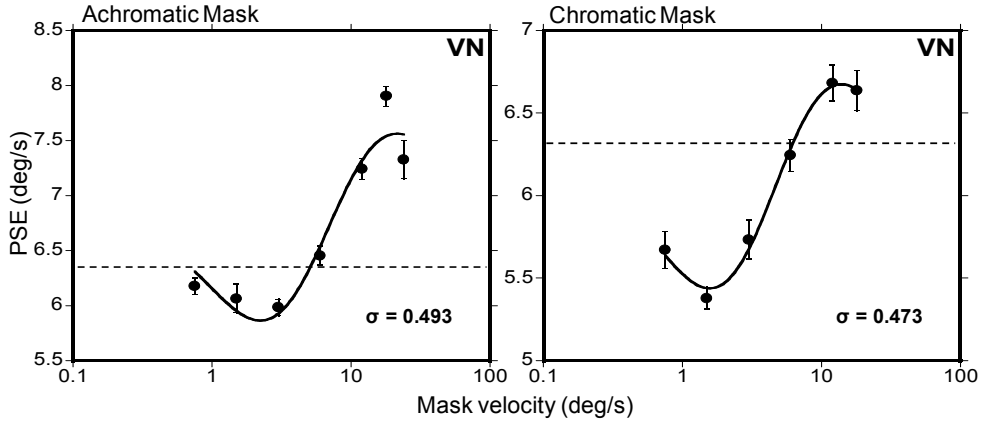


Figure 7.3 The effect of mask velocity in case of luminance and chromatic grating masks in case of a reference of 6 deg/s velocity. PSE values are plotted as a function of mask velocity. Data from one observer (VN), fitted with the 1st derivative of the Gaussian function. Error bars indicate errors of the logistic curve fits.

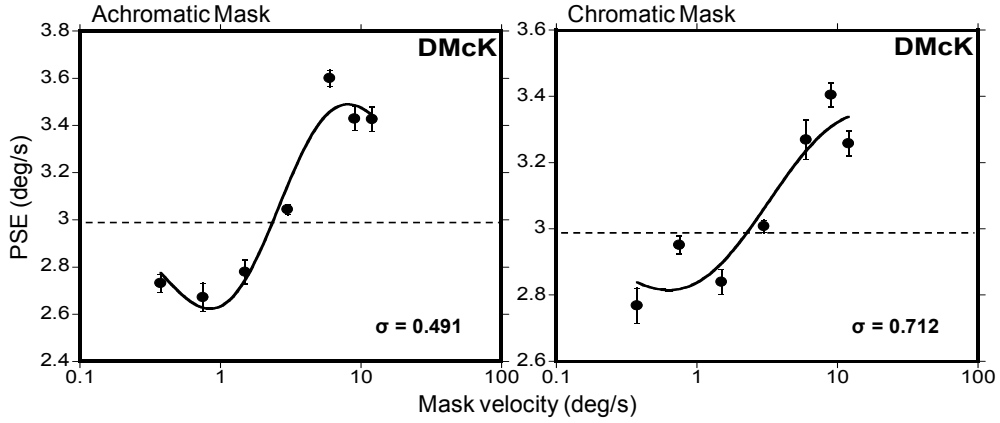


Figure 7.4 The effect of mask velocity in case of luminance and chromatic grating masks in case of a reference of 3 deg/s velocity. PSE values are plotted as a function of mask velocity. Data from one observer (DMcK), fitted with the 1st derivative of the Gaussian function. Error bars indicate errors of the logistic curve fits.

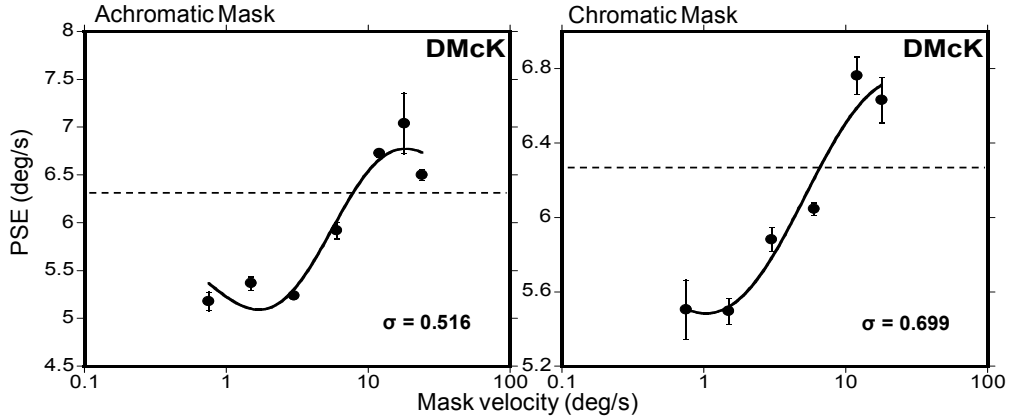


Figure 7.5 The effect of mask velocity in case of luminance and chromatic grating masks in case of a reference of 6 deg/s velocity. PSE values are plotted as a function of mask velocity. Data from one observer (DMcK), fitted with the 1st derivative of the Gaussian function. Error bars indicate errors of the logistic curve fits.

Figures 7.6 - 7.9 show how speed discrimination ability for luminance gratings, change as a result of achromatic or chromatic mask stimuli of varying velocities. According to the data, neither mask velocity nor chromatic content have any apparent or consistent effect on discriminative ability, thresholds remain at a level similar to that obtained in the absence of a mask stimulus.

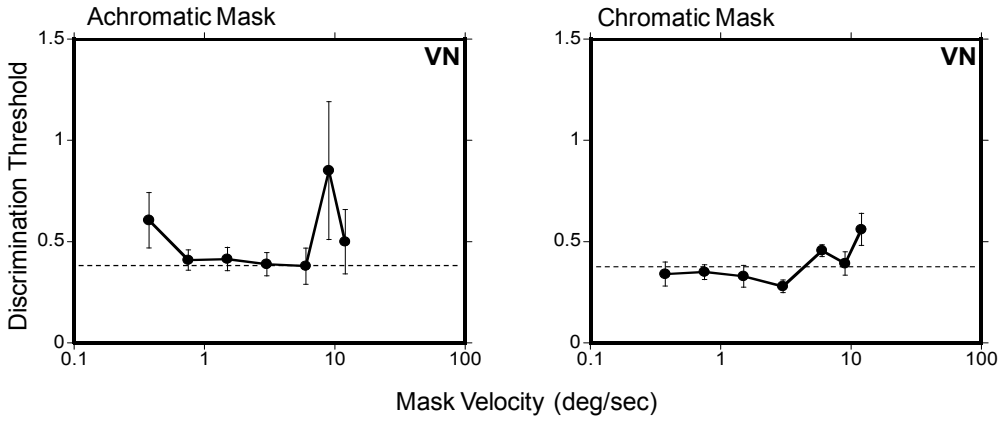


Figure 7.6 The effect of mask velocity in case of luminance and chromatic grating masks in case of a reference of 3 deg/s velocity. Discrimination threshold values are plotted as a function of mask velocity. Data from one observer (VN). Error bars indicate errors of the logistic curve fits.

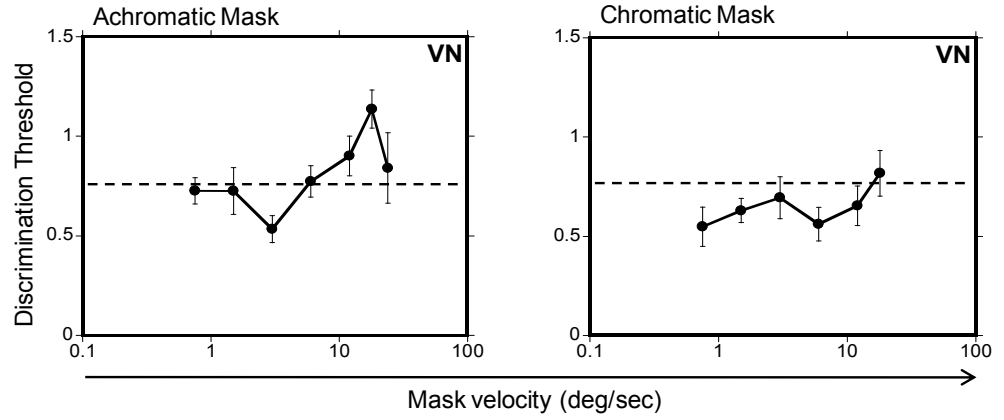


Figure 7.7 The effect of mask velocity in case of luminance and chromatic grating masks in case of a reference of 6 deg/s velocity. Discrimination threshold values are plotted as a function of mask velocity. Data from one observer (VN). Error bars indicate errors of the logistic curve fits.

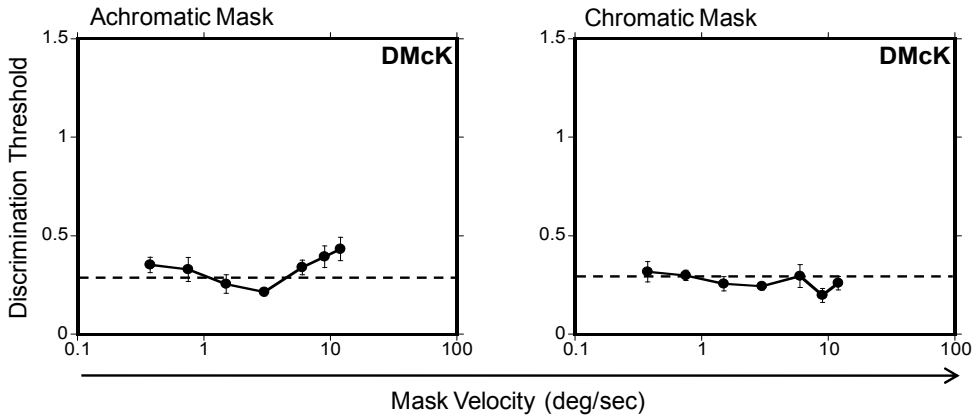


Figure 7.8 The effect of mask velocity in case of luminance and chromatic grating masks in case of a reference of 3 deg/s velocity. Discrimination threshold values are plotted as a function of mask velocity. Data from one observer (DMcK). Error bars indicate errors of the logistic curve fits.

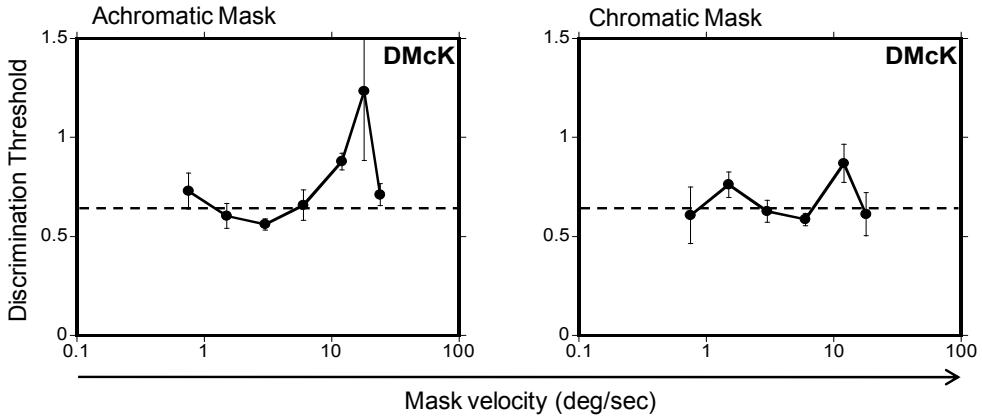


Figure 7.9 The effect of mask velocity in case of luminance and chromatic grating masks in case of a reference of 6 deg/s velocity. Discrimination threshold values are plotted as a function of mask velocity. Data from one observer (DMcK). Error bars indicate errors of the logistic curve fits.

7.2.4 Discussion

In this experiment we have shown speed specific masking effects in VSTM that were independent of the chromatic content of the interfering stimuli. This stimulus selectivity for speed is in agreement with behavioural studies that have shown that in case of VSTM for speed, mask stimuli that have similar speeds as the reference are able to disrupt the fidelity of the stored representation in a delayed discrimination task, while others are not able to do so (Magnussen & Greenlee, 1992; McKeefry et al., 2007). Similar speeds bring about a

deterioration in performance, whereas memory masks that have the same speed as the reference do not result in any change in performance as expressed by the alterations in the perceived speed of the remembered stimuli. This finding is in agreement with previous studies that provided evidence for the existence of multiple separate memory mechanisms, each being selective for a given range of stimulus speeds (Bennett & Cortese, 1996; Lalonde & Chaudhuri, 2002; Magnussen & Greenlee, 1992; Magnussen et al., 1991; Magnussen et al., 1996). Based on this notion, it is plausible that stimulus parameters that are stored within the same mechanisms are capable of causing interference, whereas the ones that belong to separate stores are not able to interact.

The finding that there is no difference between the chromatic and achromatic mask effects might imply that the retention of velocity information in VSTM is independent of chromatic and luminance content. This indicates that VSTM mechanisms for speed are able to utilize chromatic and luminance information in the analysis of speed. One reason for this phenomenon might be that the processes of memory masking in VSTM occur at a level where colour and motion signals are combined. One possible location for that might be MT/V5, which is known to have a role not only in the processing but also in the storage of information about the speed of visual stimuli. This area would then serve as an anatomical substrate for the link between sensory and memory processes in vision and VTSM.

In motion processing, it has been shown that VSTM is selective for the speed of the stimuli instead of its spatiotemporal characteristics which suggests that VSTM for speed is supported by areas that are located beyond V1, possibly at the level of V5/MT (Magnussen & Greenlee, 1992; McKeefry et al., 2007;

Perrone & Thiele, 2001; Tolhurst & Movshon, 1975). The involvement of higher cortical areas in visual perceptual working memory is a currently widely accepted notion. According to this view, in VSTM the sensory and memory areas work together in a network, that has a dual function, sensory encoding and the storage of information (Bisley & Pasternak, 2000; Fuster, 1997; Magnussen & Greenlee, 1999; Pasternak & Greenlee, 2005). Area V5/MT has a fundamental role in the sensory processing of motion and evidence seems to suggest the same is the case in VSTM for motion, so it might serve as a link between sensory and memory processes (Bisley et al., 2004; Liu & Newsome, 2005; McKeefry et al., 2007; Perrone & Thiele, 2001).

We have also shown that there is no difference between the ability of luminance and chromatic memory masks to disrupt the stored representation of the velocity of the remembered stimulus. There seems to be the same pattern of interference between luminance and colour inputs as between luminance and luminance inputs. This finding denotes that there is probably a mutual mechanism that is exploited in case of the retention of the speed of stimuli that is characterized by either chromatic or luminance information. This suggests that the integration of this information takes place at the level of the storage mechanisms, or the integration is accomplished at an earlier sensory processing stage, for example at the level of V5/MT, where some of the cells have been shown to respond to motion that is defined by colour or luminance (Albright, 1992; Barberini et al., 2005; Dobkins & Albright, 1994; Ffytche et al., 1995b; Gegenfurtner et al., 1994; Seidemann et al., 1999; Thiele et al., 1999, 2001).

In summary, in this chapter we have examined VSTM for speed with special interest on the processing of luminance and colour information employing a

memory masking paradigm. As in the previous chapters, we have found mask specific changes in the stored representation of velocity information and this masking effect was independent of the chromatic content of the mask. These results imply that chromatic and luminance information are integrated in VSTM for speed.

Chapter 8

Conclusions and Future Work

8.1 Introduction

In this chapter a summary of the results and conclusions of this thesis is presented and ideas for future experiments are discussed which would attempt to provide a more complete evaluation regarding the organisation of human perceptual memory.

The aim of this thesis was to carry out a comprehensive study of the organisation of visual information in VSTM for a range of stimulus dimensions such as colour, spatial frequency, contrast and speed. According to recent views on human perceptual short term memory, sensory and memory mechanisms interact in VSTM, and the representation of the remembered visual stimulus is linked with visual discrimination mechanisms. Evidence shows that the characteristics of VSTM for certain stimulus parameters rely on implicit memory since it does not appear to depend on conscious recall. Traditional views regard VSTM as a single, attention dependent limited capacity storage system that is short lived and aids the construction of high fidelity long term representations and it provides input to the perceptual representation system

(Magnussen, 2009; Schacter et al., 2000), which is known to be an implicit system contributing to object identification. Visual perceptual memory, as proposed by Magnussen (Magnussen, 2009) is probably responsible for the storage of visual information at a low-level in the cortical processing hierarchy and works in close correlation with sensory discrimination mechanisms. Evidence for this viewpoint comes from psychophysical experiments, which have shown that delayed discrimination ability matches the accuracy of the perceptual discrimination performance (Magnussen, 2000; Magnussen & Greenlee, 1999). A characteristic property of visual information that is retained within low-level perceptual memory is that it is fragile and vulnerable to interference. This suggests that there exists a weak or fragile form of visual short term memory (VSTM) in which information is initially stored (Sligte et al., 2008, 2009).

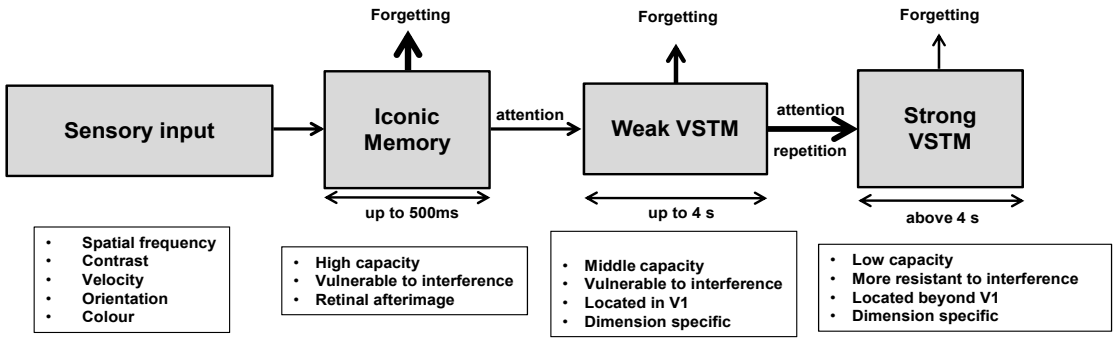


Figure 8.1 The transfer of sensory information to short term memory.

The transfer of low-level sensory information into memory is a multi-stage process, there are further subcategories within VSTM depending on the timescale and stability and capacity of the mechanisms (**Figure 8.1**) (Sligte et al., 2008, 2009). Based on experimental data, three stages of visual processing emerges that work alongside each other and in which the robustness of the representation depends on the amount of attention that is devoted to the task (**Figure 8.1**) (Sligte et al., 2009).

Iconic memory is a fragile and short lived representation that can be easily disrupted by simple stimuli, which suggests that iconic memory is more like a retinal afterimage, or a positive afterimage of the just seen image. The amount of information iconic memory is able to hold however, is unlimited. According to recent views, depending on the amount of attention devoted to the task the memory representation of a visual stimulus can be either held in a weak type of VSTM or a more robust type of VSTM (Sligte et al., 2009). The retained information in weak VSTM can be disrupted or altered by an interfering (i.e. memory mask) stimulus that has similar attributes to the reference stimulus, but is resistant to simple, non-relevant stimuli, which suggests that this representation has its substrates at the level of or higher than the visual cortex. Fragile VSTM has a relatively high capacity, subjects are able to hold much more than four visual stimuli in memory (Sligte et al., 2008). When sufficient attention is devoted to the stimulus (amount of concentration), information from the fragile VSTM representation is transferred to the robust VSTM, at about 4 s into the memory delay. This robust or traditional VSTM is able to hold only up to four visual objects, therefore its capacity is highly limited but is very resistant to interference. It has to be noted though, that overall, the capacity of these two types of VSTM representations are highly dependent on the complexity of the stimulus, therefore there is no clear cut categorization as to the number of items that are held by each of these mechanisms (Sligte et al., 2008).

A recent study has found correspondence between the strength of representation (iconic, fragile and robust VSTM) and the activation level found in V4 (Sligte et al., 2009), which implies that neuroimaging can predict, based on the activation pattern, where the visual information is mostly stored, namely, in iconic, weak or strong VSTM mechanisms. V4 shows the strongest activation

when an item is in robust VSTM, intermediate level of activation for weak VSTM and minimal activation when memory is not active, such as during perception. V4 is known to be responsible for the encoding of the stimuli (Sligte et al., 2009) and also has a role in attention. The activation in V1 - V3 in this experiment did not correlate with the type of memory used. Interestingly, another study found attention, but not memory related activation in V1 (Offen et al., 2009).

The neural substrates of fragile VSTM are located mostly in the sensory visual areas, and therefore the iconic memory and fragile VSTM can also be imagined as a perceptual representation that is converted into memory representation when attention resources are allocated. In the same way, the robust form of VSTM provides a reserve from which perceived visual stimuli in memory are directly accessible from higher cortical areas, which are located relatively early in the cortical processing hierarchy (Sligte et al., 2008).

According to Magnussen (Magnussen, 2009), visual perceptual memory has certain distinct characteristics. There are different stores that carry out the analysis of the various stimulus attributes separately, i.e. they exhibit a modular organisation, and there is lateral inhibition within elements of stimulus dimensions that belong to the same store. The separate storage systems are connected with separate mechanisms in perceptual processing as well. The perceptual and memory processing exploit cortical resources that are located at the level and beyond V1 but early in cortical processing. Dual discrimination experiments, memory masking, and brain imaging studies provide experimental evidence in support of these concepts (Magnussen, 2009).

According to recent evidence, visual information held in short term memory is retained mainly by the sensory areas that are located relatively early in visual processing (Magnussen, 2009; Pasternak & Greenlee, 2005). Visual short term

memory is devoted to the retention and usage of visual information and is connected with several cognitive functions such as intelligence (Desimone & Duncan, 1995; Fukuda et al., 2010) and emotional self-regulation (Kang et al., 2011; Schmeichel & Demaree, 2010). Information in VSTM is held in the early visual areas such as V1 (Harrison & Tong, 2009; Serences et al., 2009), which suggests that visual and memory areas are interconnected and this might imply that our memories have an influence on how we perceive the world (Kang et al., 2011). Studies have shown that memorandi influence the distribution of attention (Desimone & Duncan, 1995; Soto et al., 2008; Woodman et al., 2007) but the same is yet to be shown in case of perception (Kang et al., 2011). In a recent psychophysical study (Kang et al., 2011) this question was investigated in order to examine whether information held in VSTM alters the perceived visual stimuli in the case of motion direction discrimination, by exploiting the motion repulsion effect in a memory recall task (Hiris & Blake, 1996; Marshak & Sekuler, 1979). Kang et al. hypothesised that if there is an effect then the perceived direction of the motion stimuli would show a systematic shift away from that of the memorized one (Kang et al., 2011). They have shown that a retained representation of a moving dot stimulus in visual perceptual memory alters the perceived direction of a moving stimulus that is presented to the observer (Kang et al., 2011). Their finding shows that the direction of motion that is retained in memory alters the perceived direction of a presented moving random dot stimulus. One question remains, how is this interaction is mediated? One possible way could be by means of focusing attention to the memoranda during the task (Kang et al., 2011; Olivers et al., 2011).

The finding that memory alters perception is highly relevant to our study, since we have found similar, stimulus specific effects by employing a memory

masking paradigm in delayed matching tasks (Kang et al., 2011). In our paradigm, the memory representation was altered by the perception of an additional stimulus (i.e. memory mask) during the memory interval in a mask specific pattern. Possible reasons for this phenomenon most likely lie in the specific organisational features in visual short term memory, namely, that in VSTM, there are parallel mechanisms, each devoted to the analysis of a single visual dimension, and within each of these mechanisms there are multiple channels that carry out the processing of given ranges of stimulus values. This organisation mirrors that found in sensory adaptation experiments for the existence of multiple spatial frequency channels, and we have also found evidence for this organisational principle in the colour, spatial frequency and motion domains.

In the literature on brain imaging of perceptual memory, studies have shown a strong activation during the memory delay in delayed discrimination tasks in V1 (Baumann et al., 2008; Harrison & Tong, 2009; Magnussen, 2009; Pasternak & Greenlee, 2005; Serences et al., 2009). Serences et al. (Serences et al., 2009), however found consistent stimulus specific activation in V1 with pattern specific analysis. Harrison and Tong (Harrison & Tong, 2009) found orientation specific activation in V1 in a delayed matching task and increased activation as well in other early visual areas (V2, V3, and V4) during the first few seconds of the memory interval (Harrison & Tong, 2009). Baumann found an overall stronger activation in V1 and V2 when an irrelevant feature (gratings of different orientations) was presented while the spatial frequencies of the gratings were compared after the memory delay (Baumann et al., 2008). Some other studies, however found increased activation in tasks that required attention as opposed to memory maintenance (Offen et al., 2009).

The neuroimaging studies that also examined the degree of involvement of sensory areas in VSTM are not consistent in terms of the results. Different studies employing different paradigms and analysis techniques came up with different results (Harrison & Tong, 2009; Offen et al., 2009; Serences et al., 2009). Sneve et al. suggested that this phenomenon (i.e. relatively lower activation levels in V1 in some tasks) might be due to lateral inhibition between neurons i.e. neurons that process stimulus dimensions that are not relevant to the task are suppressed while the neurons that store the relevant features are activated ('lateral suppression effect') (Sneve et al., 2011). The memory masking stimulus carries irrelevant stimulus features therefore, based on this model, would evoke a lesser BOLD response in V1. This idea was explored in a delayed memory masking paradigm. The different processing channels that exist within each stimulus dimension seem to interact with each other in an inhibitory manner that results in the lessening of the memory related activity in V1 (Sneve et al., 2011). This effect was only observed in V1 and was consistent in case of all examined participants.

8.2 Conclusions

In this section I summarize the main findings of this work. In **Chapter 4** we examined the differences in the fidelity of the retained information in VSTM for colour in case of perceptual colour categories such as unique-, cross-over hues and for colours that are defined by the cone opponent mechanisms. These colours were chosen with the aim of examining memory performance in relation to the underlying organisation of colour information in sensory processing. Memory performance was quantified by measuring changes in accuracy, discrimination threshold and hue shifts as a result of increasing time delays of

up to 10 s. We have found that the decay in VSTM for colour during the first 10 s of retention interval is less marked in case of the perceptual colour categories, as indicated by smaller hue shifts. Colours defined by the cone opponent mechanisms underwent larger hue shifts in memory in all cases. This finding might denote that there is a link between short term memory for colour and colour appearance mechanisms (i.e. higher order colour perception), which might form the basis of colour storage in short term memory. The results were invariant even when the values were converted to a perceptually uniform colour space, such as CIE Lu'v', therefore our deductions were not affected by the limitations of the colour space we used (MBDKL/CIE 1931 xy).

In **Chapter 5** we examined colour VSTM in the context of the underlying sensory physiology and in view of the recent emphasis on the close links between the neural mechanisms that underlie the analysis of sensory information and those involved in its retention in short term memory. We employed interfering or 'memory masking' stimuli of variable parameters such as colour, luminance and saturation and measured how performance on a delayed hue discrimination paradigm was affected as expressed by changes in discrimination thresholds and PSEs. We have found evidence for the selective nature of masking effects in the colour domain. We have found narrowly tuned memory masking effects that are comparable to higher order, non-linear colour tuning mechanisms. This provided further evidence for the possible links between perceptual colour categories and VSTM and the notion that VSTM is likely to be based on perceptual colour processing. Furthermore, we have demonstrated, using a delayed colour discrimination paradigm, the existence of selective, hue dependent, mask induced interference effects on stored representations of colour stimuli within VSTM. Perceptual memory for colour

appears to contain an array of stores that holds chromatic information across relatively limited bandwidths of colour space, there are separate memory stores for different perceptual colour categories, within which the representation of information is relatively coarse. The colour memory masking effects we have found are likely to be mediated by chromatic neurons at a cortical stage where the transformation from cone-opponent to more perceptually relevant colour coding has already taken place. We have also found stimulus selectivity for the saturation and luminance content of the remembered colour, which indicates that there might be subsystems for the representation of saturation for each colour. We have also found evidence that luminance and colour information processing is connected at some level in VSTM.

In **Chapter 6** we explored the link between sensory processing and memory stores in case of spatial frequency. Similar to the experiments in the previous chapter, we employed memory masking stimuli during the ISI in a delayed discrimination task. The mask grating was varied in terms of spatial frequency, orientation and contrast. We have found selective patterns of masking which serves as evidence for the existence of multiple, spatially tuned channels in VSTM, which further strengthens the case for visual perceptual memory being closely allied to low-level visual processing. The bandwidths of these memory masking effects were in good agreement with the results of sensory (i.e. contrast) adaptation experiments that provided measures for the bandwidths of these channels in sensory processing. We also examined the effect of spatial location and found that these selective memory masking effects hold, with little decrease in magnitude at horizontal separations up to 6°, which is a distance outside measured for contrast adaptation effects. These effects demonstrate the existence of spatially long range and long lasting facilitation effects in the

storage of spatial frequency information. Low level spatial filters do have the capability to retain information about visually presented patterns far beyond their normal limits of spatial and temporal integration and may form the basis for the storage of spatial information in memory. At the same time, these effects have a much broader range of transfer across space and orientation compared to those mediated directly by low-level sensory mechanisms, which suggests that they are likely to be supported by neural processing at a level beyond V1 where neurons have the ability to integrate across different stimulus attributes. This suggests that perceptual memory for spatial frequency operates at a level beyond V1, where size and shape constancies are computed. The retention of spatial frequency lacks orientation selectivity, the spatial frequency selective effects are independent of stimulus orientation, implying that the two kinds of information are separately processed in VSTM, differently from sensory processing, in which adaptation experiments found evidence for interconnected processing.

In **Chapter 7** we presented results from memory masking experiments for speed, employing similar experimental paradigm as in Chapters 5 and 6. We have found stimulus selectivity for speed, and these effects were independent of the chromatic content of the stimulus; the chromatic gratings had exactly the same effects as achromatic gratings, implying that memory masking for speed takes place at a stage where the two types of information, colour and luminance, are already integrated for the processing of motion.

8.3 Future Work

As has been previously discussed, VSTM is considered to be based on neural activity in a network of cortical areas that include the regions that are involved in

the sensory analysis as well as those that are responsible for the short term storage of visual information (Fuster, 1997; Goldman-Rakic, 1987; Pasternak & Greenlee, 2005). In VSTM, sensory areas retain information about their preferred stimuli, for example occipitotemporal areas are activated in visuo-spatial tasks, highlighting the roles they play in visual perception. In the ventral occipital cortex, there are numerous regions that have been shown to take part in the different stages of colour perception. V4 at the posterior region of the fusiform gyrus plays an important role in colour perception (Beauchamp et al., 1999), whereas other areas take part in colour imagery, recognition and naming (Howard et al., 1998; Price et al., 1996). One experiment we would like to perform is to examine whether V4, apart from being active in passive colour viewing tasks, is also active during the memory delay in VSTM, and also which additional areas in the ventral occipito-temporal network have a role in this process. In view of the recent findings it would also be of interest to examine which areas are more active in the different, previously discussed memory stages (i.e. iconic, fragile VSTM, strong STM). An earlier neuroimaging study has already shown the activation of V4 in a delayed match-to-sample task for colour (McKeefry & Zeki, 1998). Similarly as has been shown in case of cortical areas FFA and PPA for face and place stimuli, there should be activation in V4 for colour memory tasks (Ranganath et al., 2004).

In order to increase our understanding of the involvement of different brain areas in memory mechanisms, the next step would be to examine and locate the visual areas that are involved in the short term memory of colour with an event related functional Magnetic Resonance Imaging (fMRI) paradigm (McKeefry & Zeki, 1997b). Initially we could functionally identify V4 and other occipito-temporal areas with retinotopic mapping that take part in the perceptual

processing of colour information. Then we would attempt to identify memory related activity in V4 and examine the extent to which this area is selective for colour when compared to other stimulus dimensions.

This could be examined in two ways:

1. Using a delayed match-to-sample task we will examine its activation during non-colour related retention. We envisage that there will be minimal or no activation in V4 if we use a non-specific stimulus.

2. We could thereafter examine V4 activity in a task that requires increased activation. We aim to use an n-back test in which the memory load can be gradually increased (Ikeda & Osaka, 2007). This method was already used to prove functional segregation within VSTM (Carlson et al., 1998; Druzgal & D'Esposito, 2003). We will first present the reference stimulus to the observers and then present four different temporally separated test probes which will contain the test hue as well and the observer will have to identify when the reference was presented. In a 1-back condition the test will appear immediately after the probe whereas in the 4-back condition it will appear in the 4^{th} temporal interval. As the difficulty of the task increases the activity in area V4 will presumably increase as well.

Afterwards we would try to identify additional, previously mentioned regions in the visual pathway that could be of interest as well to find activity that is related to the short term memory for colour.

Recent evidence in the area of VSTM research (Pasternak & Greenlee, 2005), has led to the increasing recognition that sensory areas play an important role in short term perceptual memory processes (Magnussen, 2009). This work

explored the general organisational principles of visual information and contributes to the current models of VSTM. We have found evidence in favour of the modular organisation of information in VSTM, which contributes to the view that human visual perceptual memory is based upon multiple, selectively tuned channels in case of colour, spatial frequency and speed, similar to those found in the earliest stages of visual processing for spatial frequency. Moreover, we have found evidence that these storage mechanisms are closely linked to visual discrimination mechanisms which further supports the view that low-level sensory processing mechanisms form the basis for the retention of colour, spatial frequency and velocity information in perceptual memory. We have also found evidence for the involvement of neural processes in VSTM that are located in higher visual areas. Additional studies employing brain imaging techniques would provide further information regarding the cortical substrates of perceptual memory mechanisms for the different stimulus dimensions such as colour, spatial frequency and velocity. In conclusion, the experiments presented in this thesis provide significant insight into the organization of visual information in perceptual short term memory.

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Presentations and Publications

20th Symposium of the International Colour Vision Society, 2009

A behavioural investigation of human visual short term colour memory

Poster Presentation

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Previous studies of Visual Short Term Memory (VSTM) have indicated the existence of high fidelity memory mechanisms for visual attributes such as orientation, spatial frequency, velocity and contrast in addition to colour. However, studies that have examined short term memory for colour have not produced consistent results. In this work, we assessed the effects of different time delays on the colour discrimination ability of 3 colour normal observers using a delayed match to sample task.

In preliminary experiments based on a colour categorisation process we identified 12 chromatic axes in DKL colour space, the 4 unique hues, 4 adjacent colour categories and the 4 hues that are identified by the cardinal axes of the cone opponent mechanisms. As reference stimuli we used circular patches of these 12 hues. Test stimuli were rotations away from the reference axis within a 40 degree range (+/- 20deg), we had 11 test chromatic axis per reference axis. Stimuli were equally saturated, isoluminant circular sharp edged patches of 1.5° diameter. Reference and test stimuli were presented, simultaneously and with 1, 5, 10, 15 second time delays (ISI) in a multiple probe design where 4 different chromatic axis and their corresponding test axes were combined in a random order in one experimental run.

Results were plotted as a percentage of the correct answers as a function of the chromatic axes. The increase in the retention interval resulted in an increase in discrimination thresholds and a decrease in sensitivity. However, we did not find significant or consistent hue shifts. We have been unable to identify relationships between memory performance and the different perceptual colour mechanisms.

These results suggest that there is only a small deterioration in colour memory during the course of the examined time delay.

40th Annual Meeting of the Society for Neuroscience, 2010

The retention and disruption of color information in visual short term memory

Poster Presentation

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Studies have demonstrated that the retention of information in visual short term memory (VSTM) for basic visual attributes, such as motion, can be disrupted by the presentation of masking stimuli during inter-stimulus intervals (ISIs) which are outside the range of traditional sensory masking. The selective nature of these memory masking effects suggests a modular organization for VSTM which contains parallel stores each tuned to a relatively narrow range of stimulus parameters that are closely linked to visual discrimination mechanisms. We wish to exploit this 'memory masking' effect in order to determine whether VSTM displays similar selectivity for stimulus color. We used a delayed hue discrimination paradigm in which color normal observers (n=5) were asked to discriminate between colored reference and test stimuli (small, 1.5° diameter spots) which were presented 2.5° either side of a central fixation mark and temporally separated by an ISI = 5s. Four reference hues were examined, corresponding to exemplars of red, yellow, blue and green color categories that were identified in preliminary experiments. Discrimination thresholds and hue biases were measured for this task using a two-alternative forced choice procedure in conjunction with a method of constant stimuli. Measurements were made in both the presence and absence of mask stimuli which were presented at the fixation mark during the ISI. The mask stimuli varied in hue around the equiluminant plane in DKL color space. We report a consistent mask-induced, hue-dependent disruption of performance in case of all 4 reference colors. Consistent with previous studies, color memory masking effects are 'tuned' in the respect that color discrimination thresholds are unaffected when the reference and mask hues are identical, but increase as the mask hue shifts away from the reference hue. Induced hue shifts were greatest when mask hue was different from the reference hue, but was still located within the same color appearance category. When mask hues were from different color categories the induced shifts were similar to those obtained for baseline (i.e. no mask) conditions. The selective nature of color memory masking effects suggests that within VSTM, similar to other basic visual attributes, there are separate memory stores for different perceptual color categories. This result further emphasizes the importance of basic visual processing mechanisms as the basis upon which visual information is stored in short term memory.

11th Annual Meeting of the Vision Sciences Society, 2011

Multiple Spatial Frequency Channels in Human Visual Perceptual Memory

Poster Presentation

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Current models of short-term visual perceptual memory invoke mechanisms that are closely allied to low-level perceptual discrimination processes. The purpose of this study was to investigate the extent to which human visual perceptual memory for spatial frequency is based upon multiple, spatially tuned channels similar to those found in the earliest stages of visual processing. We measured how performance in a delayed spatial frequency discrimination paradigm was affected by the introduction of interfering or 'memory masking' stimuli of variable spatial frequencies during the delay period. Masking stimuli induced shifts in the point of subjective equality (PSE) when their spatial frequency was within a bandwidth of 1.2 octaves of the reference spatial frequency. When mask spatial frequencies differed by more than this value, there was no change in the PSEs from baseline levels. This selective pattern of masking was observed for different spatial frequencies and demonstrates the existence of multiple, spatially tuned mechanisms in visual perceptual memory. Masking effects were also found to occur for horizontal separations of up to 6° of visual angle between the masking and test stimuli. These findings add further support to the view that low-level sensory processing mechanisms form the basis for the retention of spatial frequency information in perceptual memory. However, the broad range of transfer of memory masking effects across spatial location indicates more long range, long duration interactions between spatial frequency channels that are likely to rely on contributions from neural processes located in higher visual areas.

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A behavioural investigation of human visual short term memory for colour

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Abstract

We examined visual short term memory (VSTM) for colour using a delayed-match-to-sample paradigm. In these experiments we measured the effects of increasing inter-stimulus interval (ISI), varying between 0 and 10 s, on the ability of five colour normal human observers to make colour matches between a reference and subsequently presented test stimuli. The coloured stimuli used were defined by different chromatic axes on the isoluminant plane of DKL colour space. In preliminary experiments we used a hue scaling procedure to identify a total of 12 colour stimuli which served as reference hues in the colour memory experiments: four stimuli were exemplars of red, green, blue and yellow colour appearance categories, four were located between these categories and a further four were located on the cardinal axes that isolated the activity of the cone-opponent mechanisms. Our results demonstrate that there is a reduction in the ability of observers to make accurate colour matches with increasing ISIs and that this reduced performance was similar for all colour stimuli. However, the shifts in hue that were measured between the reference and matched test stimuli were significantly greater for the cardinal stimuli compared to those measured for the stimuli defined by the hue scaling procedure. This deterioration in the retention of hue in VSTM for stimuli that isolate cone-opponent mechanisms may be a reflection of the reorganisation of colour processing that occurs in the cortex where colour appearance mechanisms become more prominent.

Keywords: colour appearance, colour memory, colour vision, cone-opponency, visual short-term memory

Introduction

Visual short term memory (VSTM) is the visual component of working memory that is responsible for the temporary storage of stimulus related information during the completion of certain behavioural tasks (Baddeley, 1983, 1986). It is based upon neural activity that takes place within a network of brain areas distributed throughout the cerebral cortex that are located beyond the primary visual cortex (V1), but occur relatively early in the cortical processing stream (Magnussen and Greenlee, 1999; Magnussen, 2000). Traditionally, the prefrontal cortex was thought to be the major contributor to short term memory, but there is increasing evidence to suggest that the mechanisms that are involved in the short term storage of basic visual information are closely associated with those that perform the sensory analysis (Magnussen, 2000; Pasternak and Greenlee, 2005).

Studies of VSTM have revealed the existence of a series of parallel, high fidelity mechanisms that are linked to the retention of information relating to specific attributes of a visual stimulus such as orientation, spatial frequency, velocity and contrast (Nilsson and Nelson, 1981; Magnussen *et al*., 1985, 1991; Greenlee *et al*., 1991, 1995; Magnussen and Greenlee, 1992; Magnussen, 2000). Colour forms another important attribute of many visual stimuli and studies have shown that chromatic information can be stored in short term memory with high degrees of accuracy over relatively

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long periods of time (Burnham and Clark, 1954, 1955; Newhall *et al*., 1957; Bartleson, 1960; Siple and Springer, 1983). However, when humans view a colour and then attempt to match it from memory there is often a small but measurable difference between the original and the memory-matched colour. This decay is usually represented by hue, brightness and saturation shifts of the matched stimulus (Collins, 1932; Newhall *et al*., 1957; Nilsson and Nelson, 1981; Jin and Shevell, 1996).

The existence of an additional mechanism within VSTM for the retention of colour information, similar to those that have been demonstrated for contrast and spatial frequency, would seem to be consistent with the extent to which colour constitutes a separable submodality within visual sensory processing. In the distal visual pathway, colour information is carried by the L-M ('red-green') and S-(L + M) ('blue-yellow') cone-opponent mechanisms, which are distinct from a cone-additive luminance (L + M) mechanism. This segregation of processing within these so-called 'cardinal' mechanisms is maintained from the inner retina, via the LGN, to the input layers of the primary visual cortex (V1) (Krauskopf *et al*., 1982; Derrington and Lennie, 1984; Derrington *et al*., 1984; Hendry and Yoshioka, 1994). However, relatively early in the cortical processing of colour there appears to be a transformation away from this cone-opponent or cardinal organisation. Rather than showing broad chromatic tuning, based upon linear cone inputs, similar to LGN chromatic neurons, many V1 and V2 colour cells exhibit narrower chromatic tuning functions, the peaks of which correspond to perceptual colour categories such as red, yellow, green or blue, for example (Lennie *et al*., 1990; DeValois *et al*., 2000; Conway, 2003; Xiao *et al*., 2007). This suggests that colour processing is re-organised centrally and is based around more perceptually relevant, colour appearance mechanisms, as opposed to cone-opponent mechanisms which predominate in the sub-cortical visual pathway.

In the light of this reorganisation of colour processing in the primate cortex we wanted to examine what consequences this might have for the organisation of VSTM for colour. Up to now there has been little attempt to try and examine short term memory for colour in the context of the organisational framework outlined above. This approach seems particularly pertinent in view of the recent emphasis on the close links between the neural mechanisms that underlie the analysis of sensory information and those involved in its retention in short term memory (Pasternak and Greenlee, 2005). In particular we wanted to examine the extent to which VSTM for colour is based upon colour appearance categories that have a greater perceptual relevance, as opposed to those colours which isolate the activity of pre-cortical colour processing mechanisms.

Methods

Stimuli

The stimuli were generated by purpose built software to drive a video graphics card (VSG 2/5; Cambridge Research Systems, Rochester, Kent, UK) and displayed on a high resolution colour graphics monitor with frame rate of 120 Hz (GDM520; Sony Corporation, Tokyo, Japan). Monitor calibration was performed by using a ColourCal probe (Cambridge Research Systems Ltd.) and CIE colour correction was carried out with a PR-650 Spectrascan SpectraColorimeter (PhotoResearch, Chatsworth, CA, USA). The monitor subtended $26.3° \times 32.75°$. The background was a uniform grey of luminance equal to 12.5 cd m^{-2}, (CIE 1931 chromaticity co-ordinates; $x = 0.310$, $y = 0.316$, illuminant C). The colour stimuli consisted of hard edged circular coloured patches the chromaticities of which were specified as equal length vectors in DKL colour space which were defined by their angle of rotation (ϕ) in the isoluminant plane. The endpoints of these vectors formed a circle around illuminant C.

Observers

Five observers took part in the study (three females and two males; mean age = 36.2 years, S.D. = ±5.6 years). All had normal colour vision according to Rayleigh matches made on a HMC Anomaloskop, and the Farnsworth–Munsell 100-Hue test. All had 6/6 or corrected to 6/6 Snellen visual acuity. The experiments were performed in a darkened room and observers fixated on a small black cross on the centre of the screen which was viewed binocularly from a distance of 114 cm.

Hue scaling experiment

In preliminary experiments we performed a hue scaling procedure in order to determine the location in DKL colour space of the four colour stimuli that were reported as exemplars of four main colour categories: red, green, blue and yellow. A four-alternative forced response procedure was used where observers indicated whether the presented colour stimuli appeared blue, green, yellow or red (DeValois *et al*., 1997; Parry *et al*., 2006). We presented 20 different chromatic axes which represented vectors that were equally spaced in steps of 18° ranging from $\phi = 0°$ to $\phi = 360°$ around the white point of DKL colour space. The results were analyzed by deriving four colour naming functions *p*[red], *p*[blue], *p*[green], and *p*[yellow], where *p*[colour] was the proportion of times that a particular test hue was called that colour out of a total of 20 presentations. From these

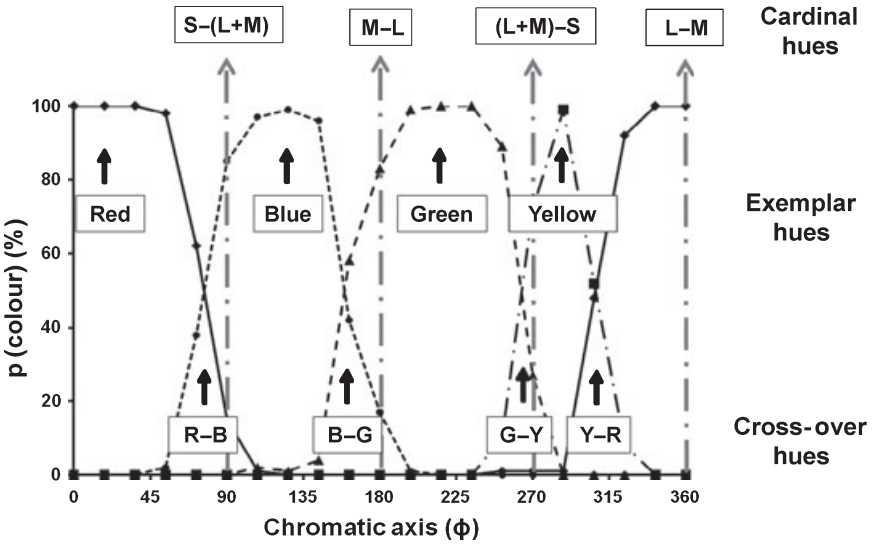

Figure 1. Group averaged hue scaling functions (n = 5) showing the chromatic axes in DKL colour space that define the 12 main chromatic stimuli that are used in subsequent experiments: four exemplar hues (red, green, blue and yellow) which are located at the central maximae of the red, green, yellow and blue functions; four cross-over hues (R-B, B-G, G-Y and Y-R); and four cardinal hues that are defined by axes which isolate cone-opponent mechanisms.

data we identified 12 colour stimuli for each observer (*Figure 1*): exemplars of four main hues (red, blue, green, and yellow) which were defined as the central maximae of the hue scaling functions, four 'cross-over hues' which corresponded to the axes in colour space where the presented stimuli were equally likely to be identified by adjacent colour appearance mechanisms (R-B, B-G, G-Y and Y-R) and 4 'cardinal hues' that corresponded to axes that isolate activity of the cone opponent mechanisms (ϕ = 90°, 180°, 270° and 360°).

Colour memory experiment

VSTM is usually examined using a delayed matching or discrimination paradigm. Studies using such tasks have shown that there is a high degree of accuracy in working memory for many different stimulus dimensions (e.g. contrast, speed, orientation, etc.) and that information is retained in memory with relatively little loss for up to 30 s (Magnussen and Greenlee, 1999; Magnussen *et al.*, 2003). A similar delayed matching paradigm was used in this study and involved the presentation of a chromatic reference stimulus chosen from any one of the 12 orientations in colour space specified following the hue scaling experiment (*Figure 1*). Following an inter-stimulus interval (ISI), a test stimulus was presented, the hue of which could fall anywhere within a pre-defined range either side of the reference hue in colour space. At the two endpoints of this range were colours that were reported as discriminable from the reference stimulus on all trials. The test stimulus located in the middle of this range was identical to the reference stimulus (*Figure 2a*).

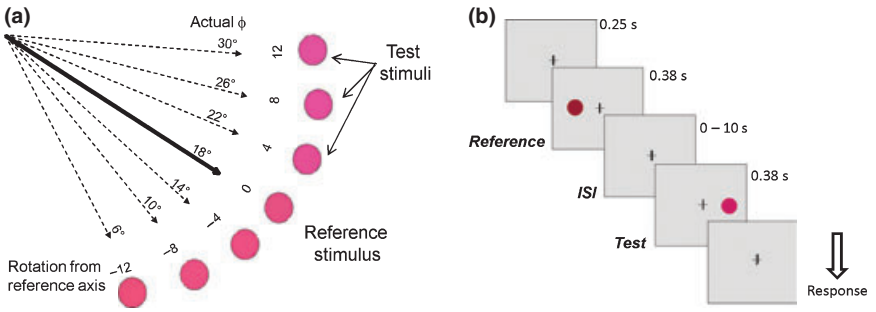

Figure 2. (a) Eleven test stimuli (not all shown) were chosen to span a range of ϕ = ±40° either side of (and including) the axis of the reference hue in DKL colour space. In this case the reference stimulus has an axis of ϕ = 18° but a similar arrangement was used for other reference stimuli. (b) The delayed match to sample paradigm: a reference stimulus was presented 1.5° to the left of a centrally placed fixation mark for 0.38 s. This was followed by an ISI which could vary between 0 s (simultaneous matching) up to 10 s. After the ISI a test stimulus was presented for 0.38 s at 1.5° to the right of the fixation point. Following the offset of the test stimulus the observer had to indicate whether the presented test hue was the same or different from the reference by a button press.

We employed 11 different test stimuli per reference stimulus and these were equally spaced within this range in steps of $\phi = 4°$. The observer's task was to indicate with an appropriate button press whether the presented test stimulus was the same or different from the reference. The reference and test patches were presented simultaneously as well as with 1, 5 and 10 s ISIs.

The stimuli were circular, had sharp edges, and their diameter subtended 1.5° of visual angle. The reference stimuli were presented 1.5° away from the central fixation point on the left side along a horizontal plane and the test stimuli were presented on the right side at the same distance along the horizontal plane (*Figure 2b*). In order to minimise rehearsal effects that would be generated by repeated exposure to the same stimulus, the reference was varied from trial to trial so the observer could not predict which stimulus had to be matched on consecutive trials. Typically, we combined four different reference hues and their corresponding test stimuli in a random order in a multiple probe design.

To analyse these data we plotted the percentage of correct matches ('same') for each hue and for each ISI as a function of rotation away from the reference axis. The data showed normal distribution as tested by the Kolmogorov–Smirnov test ($p > 0.05$). The psychometric data were fitted by a Gaussian function and *Table 1* shows the group averaged *R* values (and the standard deviations) for these fits at the different time delays. In this study we were interested in how discrimination threshold (σ) and the position of the peak in relation to the *x* axis (μ) changed as a function of ISI. The former provides a measure of the observers' ability to perform the matching task and we used a metric termed the '*memory index*' (MI_σ), given by:

$$MI_\sigma = \sigma_d/\sigma_0 \quad (1)$$

MI_σ is the memory index, σ_d is the discrimination threshold value for delayed matching and σ_0 is the discrimination threshold value for simultaneous matching performance. Threshold metrics cannot be used as an absolute measure of performance across the whole colour space because of the perceptual non-uniformities common to such spaces. In order to counteract this problem the performance for each colour axis in the delayed discrimination task was compared to performance for simultaneous colour matching. Calculation of μ provides information about the magnitude of perceived hue shift that occurs with increasing time delay between the matched and the actual hue. We calculated the average net differences between the peak positions taken at 0 and 10 s delays to compare the induced hue shifts for the 12 different hues we examined. Initially, our hue shift values were expressed as vector rotations in DKL space. In order to address the problems associated with the perceptual non-uniformity of DKL and CIE 1931 colour spaces we also expressed the hue shifts that occurred with the stimulus delays in terms of distances in the perceptually more uniform CIE $L^*a^*b^*$ space. Co-ordinates of the matched stimuli were converted from their CIE 1931 chromaticity co-ordinates into CIE $L^*a^*b^*$ space co-ordinates (Fairchild, 2005) and the distances between the simultaneous matches and the 10 s delayed matches were calculated.

Statistical analysis of the data was performed with SPSS 15.0 (SPSS Inc., Chicago, IL, USA). We performed a repeated measures three-way ANOVA on the memory index (MI_σ) data to examine: (1) the effect of ISI (two levels: 0 and 10 s); (2) differences between the groups of colour stimuli (three levels: cardinal, exemplar and cross-over hues); (3) differences between individual colour stimuli within the above colour groups (four levels per group). For the hue shift data in the three colour spaces (DKL, CIE 1931 and CIE $L^*a^*b^*$) we carried out a repeated measures two-way ANOVA to examine the following: (1) differences between the groups of colour stimuli (three levels: cardinal, exemplar and cross-over hues); (2) differences between individual colour stimuli within the above colour groups (four levels per group).

Table 1. Mean *R* values and standard deviations of the Gaussian fits to the colour matching data for the different time delays. The data represent the average across the five observers

	0 s	1 s	5 s	10 s
R_{AVG}	0.969483	0.91005	0.902433	0.8652
S.D.	0.009223	0.05208	0.058032	0.102267

Results

Figure 3 shows the averaged MI_σ values for the five observers as a function of ISI for the cardinal, exemplar and cross-over hues. In these plots an index of one indicates that colour matching performance remains unchanged with increasing ISI compared to the simultaneous matching condition. Values >1 are indicative of deterioration in performance and as can be observed in *Figure 3*, for each of the 12 chromatic stimuli tested there is a consistent increase in the memory index values as a function of ISI. We found a main effect of ISI on memory index values ($F_{1,4} = 174.67$; $p < 0.001$) for all stimuli, but there was no statistically significant difference in performance between any of the colour groups ($F_{2,8} = 1.43$; $p = 0.294$), nor between any of the individual chromatic stimuli ($F_{3,12} = 0.749$; $p = 0.544$). The sphericity assumption, as tested with Mauchly's test (*p*-level set at $p < 0.05$), was not violated in any of the conditions.

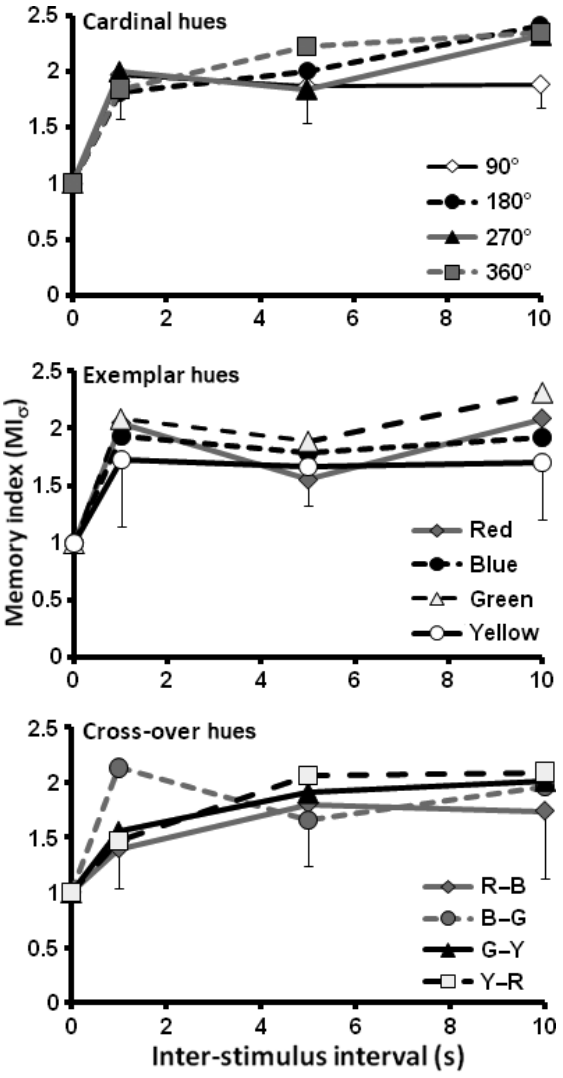

Figure 3. Memory index (MI_σ) values for the key chromatic stimuli. The figures show the group averaged data for the five observers plotted as a function of time delay. The three different categories of stimuli (cardinal, exemplar and cross-over hues) are depicted on separate graphs. The error bars represent −1 standard deviation for one dataset per graph in order to maintain clarity.

Figure 4 shows the group averaged differences in matched hues for the reference and test stimuli when they were presented simultaneously (ISI = 0) compared to the longest delay (ISI = 10 s). The magnitudes of these hue shifts are shown for all stimuli in order to qualitatively demonstrate how the perceived stimulus hues were affected by the introduction of memory delay. *Figure 4a* shows the hue shift values in DKL colour space indicating the degree of the vector rotation that was needed to make a test stimulus match the reference stimulus. *Figure 4b,c* represent the hue shifts in terms of the distance between the actual and matched stimulus co-ordinates in CIE 1931 and CIE *L*a*b** colour space, respectively. The magnitude of the hue shifts varies for the different colours, some chromatic axes undergo larger shifts than others and some require little or no rotation in order to generate a match. A significant main effect of colour group was found in all three colour spaces (DKL: $F_{2,8} = 5.60$, $p = 0.030$; CIE 1931: $F_{2,8} = 5.59$, $p = 0.030$; CIE *L*a*b**: $F_{2,8} = 4.85$, $p = 0.042$). *Figure 5* shows that this main effect is due to the higher mean for the cardinal group compared to the exemplar and cross-over groups. There was no significant difference between individual colours within the groups ($p > 0.528$ for all three spaces).

Discussion

Using a delayed matching task we have examined the extent to which information about stimulus colour can be retained by VSTM over short time delays of up to 10 s. We have measured reductions in the ability of human observers to discriminate between successively presented coloured stimuli as the temporal separation between them increases. Consistent with previous work our results point to a decay in visual short term colour memory over time (Hamwi and Landis, 1955; Newhall *et al*., 1957; Nilsson and Nelson, 1981; Perez-Carpinell *et al*., 1998). Many studies of colour memory have reported the existence of differences in the accuracy of memory across different colour or hue categories, but with no clear consistency as to which hues are retained better than others in VSTM. For example, the results of Collins (1932) indicated that certain green and red wavelengths were more difficult to remember than other wavelengths. Nilsson and Nelson (1981) concluded that violets, green-blues and yellow-orange hues were remembered better; whilst Jin and Shevell (1996) suggested that long and medium wavelength colours were remembered better than short wavelength colours. The results presented here suggest that the decay in discriminative ability over time is similar for all of the coloured stimuli that were tested.

We also assessed whether there were any differences between coloured stimuli in terms of the extent to which their remembered hues shifted away from their actual hues over time delays (ISIs). We were particularly interested in whether there were any differences between stimuli that isolated the activity of cone-opponent/cardinal mechanisms compared to those which were related to colour appearance mechanisms. Crucially, the colours that represent red, green, yellow and blue colour categories do not correspond to the cone-opponent axes, or indeed any aspect of physiological organisation that exists for colour processing in the pre-cortical visual pathway (DeValois *et al*., 1997). Whilst there may be little correlation between colour appearance mechanisms and pre-cortical colour processing, we were interested in whether the former or the latter might

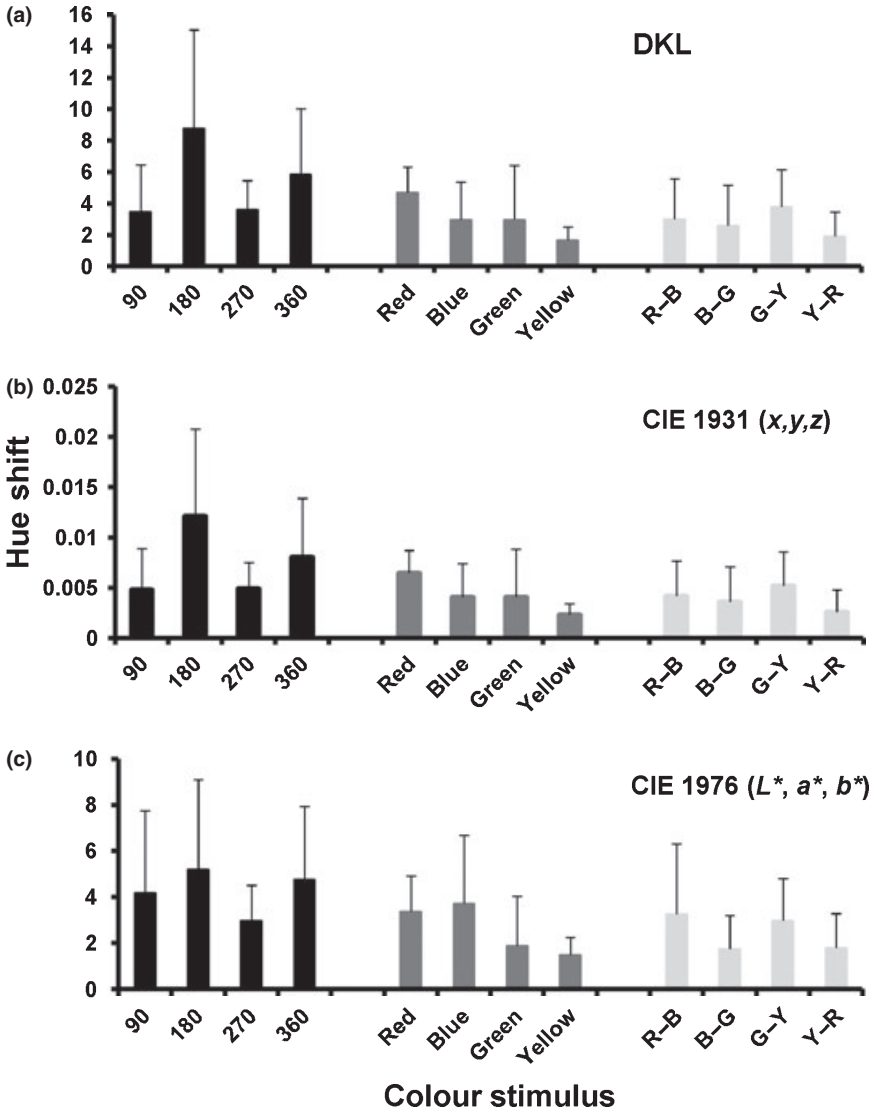

Figure 4. Hue shift values for the examined colour categories (cardinal, exemplar and cross-over hues). The figures show the group averaged hue shifts between the matches made for the 10 and 0 s ISIs in (a) DKL, (b) CIE 1931 (*x*, *y*, *z*) and (c) CIE (*L*a*b**) colour spaces. The error bars represent +1 standard deviation.

provide a basis upon which colour sensory information is organised in 'higher' cognitive functions such as short term memory. Our experiments have shown that for the longest ISI (10 s) the shifts in hue between the matched stimulus and the reference stimulus are significantly greater for the cardinal stimuli compared to either the exemplar or cross-over hues defined in the scaling experiments. This result raises the possibility that the retention of hues in VSTM that are related to perceptual colour categories are more resistant to deterioration over time than those which isolate pre-cortical processing mechanisms. Similar findings have been previously reported for focal colours which are more accurately remembered than non-focal colours (Heider, 1972). Focal colours are those that are named with the shortest response times and with consensus by many observers (Boynton and Olson, 1987). One means by which we could test the hypothesis that VSTM is based upon colour appearance mechanisms would be to use a '*memory masking*' paradigm (Magnussen and Greenlee, 1992). A crucial property of memory masking is that it only occurs when the mask and reference stimuli differ in some important respect. For example, in the spatial frequency domain, significant memory masking will only occur if the mask differs from the reference in terms of its spatial frequency by 1.5–2.0 octaves. This selectivity or tuning has been interpreted as evidence for a modular organisation of VSTM which contains parallel stores each tuned to a relatively narrow range of stimulus parameters (Magnussen, 2000). The key question is whether similar parallel, tuned stores exist for different colour categories in VSTM. Further

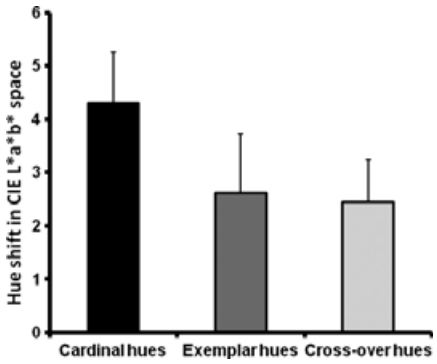

Figure 5. The hue shifts measured for the three groups of colour stimuli (cardinal, exemplar and cross-over hues). The values represent the group averaged shifts expressed in terms of the distance between the co-ordinates in CIE 1976 *L*a*b** space co-ordinates of the matches made at 10 s ISI and 0 s ISI. The error bars represent +1 standard deviation of the mean.

experiments using the memory masking paradigm might prove useful in elucidating the colour selectivity of such stores.

The importance of colour appearance mechanisms in short term colour memory points to the fact that colours are unlikely to be memorized solely on a sensory basis. The fact that perceptually relevant colour categories appear to be more resistant to shifts in their hue as a function of ISI may be indicative of an enhanced ability to apply a verbal tag to a particular stimulus that may help in the retention of colour information (Davidoff and Ostergaard, 1984). Whilst colour itself may be memorised on the basis of sensory information, work has shown that this may be strongly influenced by verbal coding (Bornstein, 1976), which neuroimaging studies suggests may involve very different cortical networks (Ikeda and Osaka, 2007). Other more long term mechanisms are also likely to be involved in how information about colour is retained in memory. Many objects that we encounter in everyday life have a typical colour that is closely associated with them, termed a memory colour. For example, when you think of a banana or strawberry you may have in mind a particular yellow or red colour, respectively. Hansen *et al.* (2006) have shown that these long term memory colours can actually influence and distort incoming colour sensory information. Therefore, the accuracy of information about colour that is retained in VSTM is likely to be the result of interactions between basic low-level, bottom-up sensory input which is subject to modification by more top-down, higher level cognitive processes.

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Multiple spatial frequency channels in human visual perceptual memory

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ABSTRACT

Current models of short-term visual perceptual memory invoke mechanisms that are closely allied to low-level perceptual discrimination mechanisms. The purpose of this study was to investigate the extent to which human visual perceptual memory for spatial frequency is based upon multiple, spatially tuned channels similar to those found in the earliest stages of visual processing. To this end we measured how performance on a delayed spatial frequency discrimination paradigm was affected by the introduction of interfering or 'memory masking' stimuli of variable spatial frequency during the delay period. Masking stimuli were shown to induce shifts in the points of subjective equality (PSE) when their spatial frequencies were within a bandwidth of 1.2 octaves of the reference spatial frequency. When mask spatial frequencies differed by more than this value, there was no change in the PSE from baseline levels. This selective pattern of masking was observed for different spatial frequencies and demonstrates the existence of multiple, spatially tuned mechanisms in visual perceptual memory. Memory masking effects were also found to occur for horizontal separations of up to 6 deg between the masking and test stimuli and lacked any orientation selectivity. These findings add further support to the view that low-level sensory processing mechanisms form the basis for the retention of spatial frequency information in perceptual memory. However, the broad range of transfer of memory masking effects across spatial location and other dimensions indicates more long range, long duration interactions between spatial frequency channels that are likely to rely contributions from neural processes located in higher visual areas.

1. Introduction

Sensory perception and memory traditionally have been viewed as very different processes that are served by very different cortical networks within the brain. However, the ability to store basic sensory information forms an important means by which an organism can retain information about its surrounding environment which can subsequently be used to mediate and guide behaviour (Baddeley, 1983, 1986, 2003). This requirement, that sensory information has to be made readily available to memory systems, has led to the proposal that the neural mechanisms that underpin this kind of memory are closely allied to those that are involved in sensory processing and may even occur in the same sensory cortical areas (Bisley & Pasternak, 2000; Fuster, 1997; Gibson & Maunsell, 1997; Graham, Barense, & Lee, 2010; Pasternak & Greenlee, 2005).

In the visual domain, the retention of information relating to basic stimulus attributes, such as spatial frequency and contrast for example, has been shown to occur within what has been termed *visual perceptual memory* (Magnussen, 2009; Magnussen & Greenlee, 1999). This form of memory can be characterised as operating in a non-declarative, implicit fashion and constitutes a pre-semantic level of storage for low-level sensory information (Magnussen, 2000, 2009). It has some (though not complete) overlap with related concepts such as: sensory working memory (Pasternak & Greenlee, 2005); the perceptual representation system (Schacter, Wagner, & Buckner, 2000; Tulving & Schacter, 1990) and visual short term memory (Magnussen & Greenlee, 1992). A key property of visual perceptual memory is that it is feature or dimension specific (Magnussen, 2000). It comprises a series of separate stores that are selective for the retention of specific visual attributes such as spatial frequency, orientation, motion, colour, and so forth (Greenlee, Magnussen, & Thomas, 1991; Magnussen & Greenlee, 1999; McKeefry, Burton, & Vakrou, 2007; Pasternak & Greenlee, 2005). This organisation mirrors that which is found right from the earliest stages in the visual pathway where the sensory processing of different stimulus attributes occurs in a similarly parallel fashion (e.g. Livingstone & Hubel, 1987). Evidence in favour of feature specificity in visual perceptual memory has emerged from psychophysical studies which, in many cases, have employed delayed discrimination paradigms. In these experiments the ability to retain information about a basic stimulus attribute is measured over a time delay or inter-stimulus interval (ISI) (e.g. Regan, 1985). The quality or fidelity of the retained information can then be indexed by any subsequent changes in performance. Using this approach, the retention of different stimulus features (contrast, orientation, spatial frequency, etc.) has been found to

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have different rates of decay with increasing ISI duration, suggesting that different perceptual memory mechanisms exist for different stimulus attributes or features (Fahle & Harris, 1992; Lee & Harris, 1996; Magnussen & Greenlee, 1999; Magnussen, Greenlee, & Thomas, 1996; Vogels & Orban, 1986). These findings are also consistent with results from 'dual-task' experiments in which observers are asked to retain information and make subsequent judgements about two stimulus features (e.g. contrast and spatial frequency). This can be done for multiple attributes virtually without impairment (Greenlee & Thomas, 1993; Magnussen & Greenlee, 1997; Magnussen, Greenlee, & Thomas, 1996; Vincent & Regan, 1995; Vogels, Eeckhout, & Orban, 1988). However, when observers are asked to make judgements about the same attribute (e.g. two spatial frequencies), then thresholds are significantly elevated (Magnussen & Greenlee, 1997). This indicates that for these tasks, interference occurs within, but not between different stimulus attributes.

The idea that perceptual memory is made up of a number of limited capacity sub-systems that independently store information relating to different stimulus attributes has also been demonstrated by the selective effects of interference or masking stimuli presented during the ISI of delayed discrimination tasks (Magnussen et al., 1991). In these so called 'memory masking' experiments increases in discrimination thresholds, induced by the introduction of masking stimuli, point to the ability of certain stimuli to disrupt the retention of information about specific stimulus features. However, these disruptions to stored representations of visual stimuli only occur when the interfering or masking stimuli differ from the remembered stimulus in some key aspect, when the mask is identical to the reference there is no disruption of performance (Magnussen & Greenlee, 1992; Magnussen et al., 1991; McKeefry, Burton, & Vakrou, 2007). An important property of memory masking is that the effects are specific to changes only along certain relevant stimulus dimensions with discrimination thresholds being unaffected by changes along other irrelevant dimensions. Furthermore, the effects are also tuned for finite ranges of these features (Magnussen et al., 1991).

In this study we employed a memory masking paradigm in order to investigate how spatial frequency information is organised within visual perceptual memory. Perhaps one of the most enduring models of low-level visual processing describes the analysis of spatial patterns in terms of the parallel operation of multiple spatial frequency filters or channels (Campbell & Robson, 1968). Experiments using pattern or contrast adaptation have played a major role in characterising these low-level sensory filters which are responsive to specific bandwidths of frequency and orientation and operate in discreet spatial locations within the visual field (e.g. Blakemore & Campbell, 1969; Blakemore & Nachmias, 1971; Georgeson & Harris, 1984). Memory masking experiments have made an analogous contribution in revealing the organisation of perceptual memory for spatial frequency. Magnussen et al. (1991), for example, have demonstrated that visual perceptual memory does exhibit spatial frequency tuning which mirrors that found in low-level vision. This finding has been central to the proposition that such memory stores are closely linked to the mechanisms that operate at the earliest stages of sensory processing (Magnussen, 2009; Magnussen et al., 1991; Pasternak & Greenlee, 2005). In this study we wanted to explore this link in more detail. One issue centres around the fact that contrast adaptation, in addition to generating increases in detection thresholds for stimuli of spatial frequency that are close (within 2 octaves) to the adapting frequency, also generate shifts in the perceived spatial frequency of subsequently viewed supra-threshold grating stimuli (Blakemore, Nachmias, & Sutton, 1970). In these experiments Blakemore and colleagues demonstrated that following a period of adaptation to grating stimuli of specific spatial frequencies, patterns with higher spatial frequencies appeared to be of higher frequency than they actually were. Conversely, subsequently presented patterns of lower spatial frequencies than the adapting frequency, appeared even coarser than they were in actuality. Thus perceived spatial frequency can be altered by prior adaptation. We wanted to examine whether a similar spatial frequency shift phenomenon exists in the domain of low level perceptual memory. Previous 'memory masking' paradigms have been largely concerned as to how discrimination thresholds are affected by the introduction of a masking stimulus during the delay period (e.g. Magnussen et al., 1991). In this study we were interested in ascertaining whether an interfering stimulus can induce a change in the 'remembered' spatial frequency. If this is the case then over what spatial frequency range is the mask effective in interfering with the retained information? If low level perceptual memory is indeed based upon spatial frequency channels similar to those found in the sensory domain then the prediction would be that these spatial frequency shifts would only occur for masking stimuli within 2 octaves of any chosen reference stimulus. Such a finding would further strengthen the case for visual perceptual memory being closely allied to low-level visual processing.

2. Methods

2.1. Stimuli

Sinusoidal luminance contrast grating stimuli were presented on a colour graphics monitor (GDM500; Sony, Tokyo, Japan; frame rate 120 Hz) controlled via a video graphics card (VSG 2/5; Cambridge Research Systems, Rochester, UK). The reference, mask and test stimuli were presented in circular windows of diameter equal to 2.5 deg, with a contrast equal to 50% on a grey (illuminant C) background of the same mean luminance (12.5 cd/m^2) (see Fig. 1). In terms of the spatial configuration of the stimuli, two versions of the experiment were performed: in the first, *spatially coincident version*, the reference, mask and test stimuli were all presented at the same retinal location centred on the fixation point. In the second, *spatially non-coincident version*, the reference stimulus was presented with a horizontal displacement to the right of the central fixation mark; the mask stimulus was presented at the fixation mark and the test stimulus was placed horizontally displaced to the left of fixation. The magnitude of the displacements from the fixation point varied up to a maximum of 6 deg. During the presentation cycle fixation was maintained on a central fixation cross.

2.2. Procedure

A delayed spatial frequency matching paradigm (Fig. 1) was used to measure performance and employed a two-alternative forced choice procedure in conjunction with a method of constant stimuli. Each trial began with the presentation of a reference stimulus of set spatial frequency (typically 1 c/deg, 3 c/deg or 5 c/deg, depending upon the experiment) which was presented for 380 ms (see Fig. 1). This was followed by an inter-stimulus interval (ISI) of 5 s during which masking stimuli of different spatial frequencies were presented for 2 s. At the end of the ISI a test stimulus was presented for 380 ms the spatial frequency of which was selected randomly from one of seven different levels which spanned a range above and below the reference spatial frequency. The offset of the test stimulus was marked by an auditory cue at which point the participants were required to indicate, using a response box (model CB3; Cambridge Research Systems), whether the test stimulus was perceived to be of higher or lower spatial frequency than the reference. In order to prevent the representation

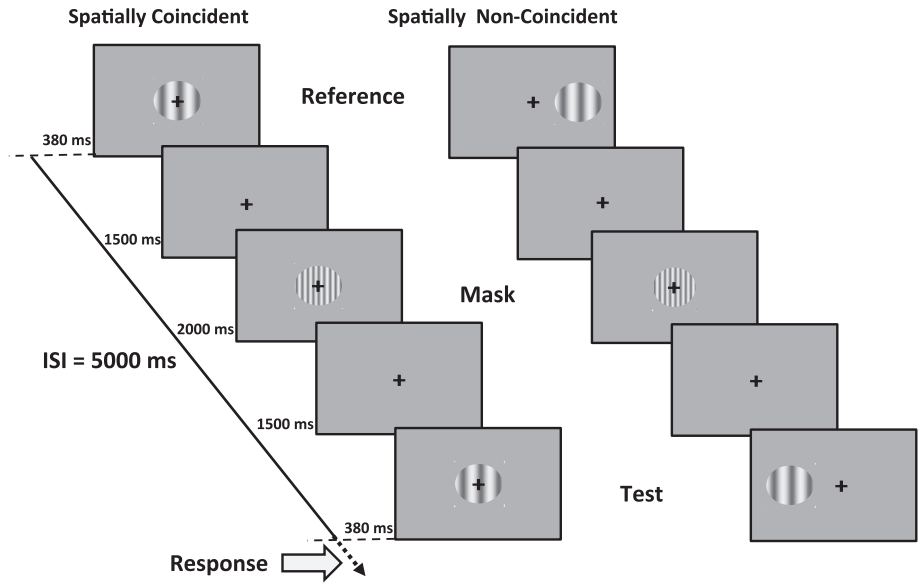

Fig. 1. A schematic representation of the delayed spatial frequency discrimination paradigm used in this study. Each cycle began with the presentation of a reference stimulus (1, 3 or 5 c/deg) for 380 ms. Following the presentation of a blank screen for 1500 ms a mask stimulus was displayed for 2000 ms. After another 1500 ms presentation of a blank screen a test stimulus was presented and at the offset of this stimulus the observer was instructed to respond by button press whether they judged the test to be of higher or lower spatial frequency than the reference stimulus. Following the response the next presentation cycle began. There were two forms of the experiment: (A) a spatially coincident version where the reference, test and mask stimuli were all presented at the same spatial location centred on the fixation point and (B) a spatially non-coincident version where the stimuli were horizontally displaced from one another by separations of up to 6 deg.

of stimulus features being built up in long-term memory over consecutive trials we introduced small random increases and decreases in the contrast (between ±10%) and spatial phase (between ±90 deg) of the test and reference stimuli. These variations were balanced over the trials to minimise any bias (Magnussen & Greenlee, 1992).

2.3. Curve fitting

The psychometric data were fitted by a logistic function of the form:

$$y = \frac{100}{\left(1 + e^{\frac{(x-\mu)}{\theta}}\right)} \quad (1)$$

where y is the percentage of times the test was perceived as being of higher spatial frequency than the reference, x is the spatial frequency of the test stimulus, μ is the spatial frequency corresponding to the 50% level on the psychometric function (i.e. the point of subjective equality (PSE)) and θ is an estimate of the spatial frequency matching threshold. This final value (θ) was divided by the reference spatial frequency to give a Weber fraction for spatial frequency discrimination ($\Delta fx/fx$). Each psychometric function was based upon 70 trials (7 levels, 10 repetitions of each level) and the logistic curves were fitted to an average of at least three of these functions.

The resulting PSE data were plotted as a function of mask spatial frequency and fitted by a first derivative of a Gaussian function described by the equation:

$$y = y_{pos} + \left[\left(A * \log\left(\frac{x}{x_{pos}}\right)\right) * e^{-\left(\frac{\left(\log\left(\frac{x}{x_{pos}}\right)\right)^2}{2\sigma^2}\right)}\right] \quad (2)$$

where y is the point of subjective equality (PSE), x is the spatial frequency of the mask, σ is the standard deviation of the Gaussian, A is a constant related to the amplitude of the function and x_{pos}, y_{pos} is the origin of the function (when $x = x_{pos}$, PSE = y_{pos}). The maxima and minima of this function occur at mask spatial frequencies $\pm\sigma$ units from the origin (i.e. $x/x_{pos} = \pm\sigma$). The half amplitude of this function represents the magnitude by which the PSE deviates from baseline.

2.4. Observers

A total of five observers took part in the experiments; two were authors (DM, VN) and the remaining three (FF, JH and PS) were naive to the aims of the study. The experiments were performed binocularly at a viewing distance of 114 cm. The observers had their viewing positions stabilised by a chin rest and their foreheads were supported by rest that restricted, but did not completely immobilise, head movement. Data were collected during four 2 h sessions in which the participants completed 610 trials in each session. Prior to the start of data collection the observers completed 140 practice trials in order to familiarise them with the experimental procedure.

3. Results

3.1. Spatial bandwidth of memory masking

Fig. 2 shows the group averaged results from an experiment where participants performed the delayed spatial frequency matching task for a reference stimulus of 5 c/deg in the presence of different mask stimuli ranging from 1 to 15 c/deg. Fig. 2A shows how discrimination threshold varies as a function of the mask spatial frequency. These data replicate the findings of Magnussen et al. (1991) and demonstrate the spatial frequency selectivity, in terms of the effects on discrimination thresholds, that occurs for the memory masking paradigm. When the mask spatial frequency is close to that of the reference stimulus, performance is minimally affected and thresholds are similar to those obtained when no mask is presented during the ISI (horizontal dashed line). However, as the mask spatial frequency starts to shift away from that of the reference, either in a lower of higher direction, then thresholds

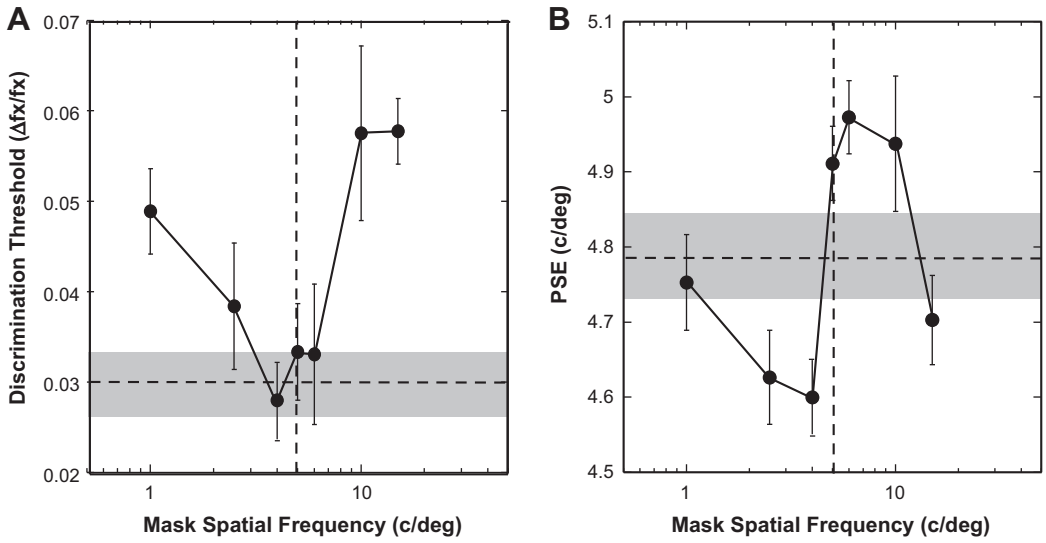

Fig. 2. Group averaged results (n = 3) for a delayed spatial frequency discrimination experiment (reference = 5 c/deg) where mask stimuli of variable spatial frequency were presented during the 5 s ISI. (A) Shows the variation in discrimination threshold as a function of mask spatial frequency. (B) Plots PSE as a function of mask spatial frequency. In these and subsequent plots the horizontal dashed lines refer to the level of (baseline) performance when no mask stimulus was introduced during the ISI. The grey area above and below this line represents ±1 S.D. of the mean performance for this condition. The vertical dashed line represents the reference spatial frequency and error bars refer to ±1 S.D. of the mean.

increase giving rise to a characteristic 'V-shaped' function that is approximately centred on the reference spatial frequency.

Fig. 2B illustrates how PSE varies as a function of mask spatial frequency relative to the baseline condition (i.e. when no mask is present). For mask spatial frequencies below that of the reference, perceived equality between reference and test occurs at spatial frequencies that are lower than the baseline PSE. Conversely, when the mask frequency is greater than the reference PSE are greater than for the baseline condition. Either side of the reference spatial frequency the perceived shift in the PSE reaches a local maximum (for higher mask frequencies) and local minimum (for lower mask frequencies). When the mask spatial frequency moves even further away from the reference the perceived shifts in the PSE decrease in magnitude and return back towards baseline values. Thus the perceived shifts in the matched spatial frequency appear highly dependent upon the spatial frequency of the masking stimuli. If the mask spatial frequency differs by a small amount from the reference stimulus, the resultant PSE is 'pulled' towards the spatial frequency of the mask stimulus. If, however, the difference between the reference and mask spatial frequency becomes too great then the effect is reduced and the PSE starts to return to values closer to those obtained under no mask conditions – as if the mask stimulus can be ignored or discounted if the spatial frequency difference between it and the reference is too great.

The spatially tuned nature of these PSE changes prompted us to fit this data with functions that were first derivatives of Gaussian functions (see methods). These functions have the advantage of providing an estimate of the bandwidth of the effects in terms providing a value (σ). Fig. 3 shows results obtained from three individual observers whose data have been fitted with these curves giving values for σ = 0.638, 0.453 and 0.543 octaves for observers FF, VN and DM, respectively. Similarly tuned functions were also obtained when the memory masking experiments were repeated for different reference spatial frequencies (1 and 3 c/deg) and the group averaged data fitted with the same first derivative Gaussian functions, are shown in Fig. 4.

The induced shifts in the remembered spatial frequency of the reference stimulus demonstrated here using the 'memory masking' paradigm mirror the kind of effects that also occur with contrast or pattern adaptation experiments (Blakemore, Nachmias, & Sutton, 1970). In these experiments prolonged exposure to a particular spatial frequency alters the perceived frequency of subsequently viewed grating stimuli. Results from these adaptation experiments have been central to the formulation of models of spatial vision processing that rely upon the existence multiple filters or channels that are responsive to relatively narrow spatial frequency bandwidths. In Fig. 5 data from Blakemore, Nachmias, and Sutton (1970) have been re-plotted in order to show how the perceived spatial frequency of various test stimuli vary following prolonged exposure to either a 3 c/deg (Fig. 5A) or a 5 c/deg (Fig. 5B) grating. As in the case of the 'memory masking' data shown Fig. 3 these contrast adaptation data show a similar dependency as a function of test spatial frequency and have been fitted by first derivatives of Gaussian functions which generates values of σ = 0.60 octaves for the 3 c/deg data and 0.66 octaves for the 5 c/deg data.

3.2. Location specificity of memory masking

In order to rule out the possibility that this spatially tuned effect of the memory masking stimulus is not simply down to local adaptation we examined the extent to which memory masking was specific to retinal location. A number of studies have demonstrated that the effects of contrast adaptation on sensitivity for subsequently presented test stimuli are highly localised to the retinal areas that have experienced adaptation (Ejima & Takahashi, 1984, 1985; Williams, Wilson, & Cowan, 1982). Decreases in sensitivity for grating patterns are greatest when adapting and test stimuli are spatially coincident but as the spatial separation between them increases to greater than 1 cycle (0.33 deg for a 3 c/deg stimulus) the shifts in sensitivity are minimal. For separations greater than this magnitude there may even be facilitation, i.e. increases in sensitivity in retinal areas immediately surrounding the region of adaptation. Beyond 12 cycles (3.96 deg for a 3 c/deg stimulus) the after-effects induced by spatially localised adaptation disappear (Ejima & Takahashi, 1984). Fig. 6 shows the results from a delayed spatial frequency matching task where the reference, mask and test stimuli appeared at different non-overlapping locations (horizontal separation = 6 deg) across the visual field. As can be observed the effects of the different masking stimuli exhibit similar spatial frequency tuning to that found when the reference, mask and test

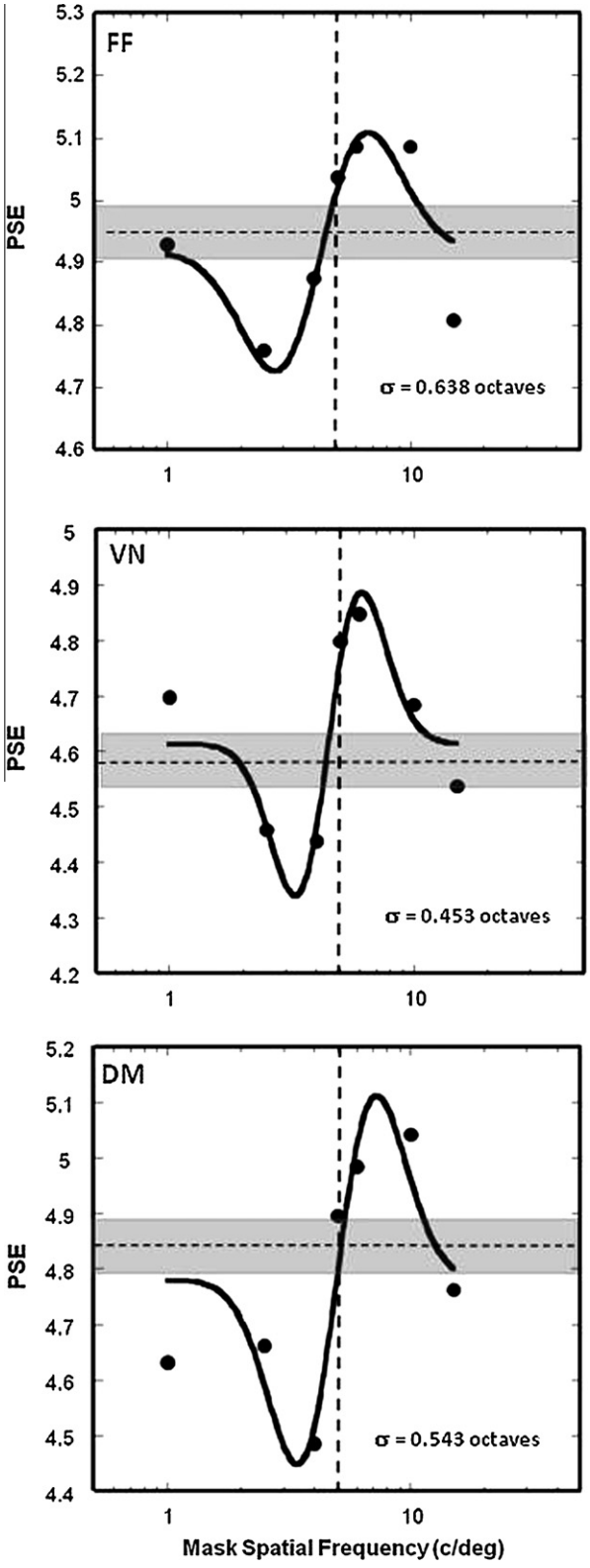

Fig. 3. PSE data plotted as a function of mask spatial frequency for three observers who performed a delayed spatial frequency matching paradigm (reference = 5 c/deg). The data have been fitted by a first derivative of a Gaussian function (see text) which provides an estimate of bandwidth (σ) for each function given in octaves.

stimuli were spatially co-incident and curve fits generated bandwidth estimates (σ) equal to 1.202, 1.196 and 0.664 octaves for the 1, 3 and 5 c/deg reference stimuli, respectively.

The data shown in Fig. 7 demonstrate that perceived shifts in matched spatial frequency for a reference stimulus of 3 c/deg that are induced by effective masks (1.5 and 6 c/deg) still occur for stimulus separations up to 6 deg without any diminution in magnitude. This non-spatially localised property of memory masking therefore differs markedly from that exhibited by contrast adaptation (Ejima & Takahashi, 1984).

3.3. Orientation specificity of memory masking

Another important property of perceived shifts in spatial frequency that occur following contrast adaptation is that the effects are orientation specific (Blakemore, Nachmias, & Sutton, 1970). Perceived shifts in spatial frequency only occur for test stimuli that are within a range of approximately ±40 deg of the orientation of the adapting grating. We therefore wanted to examine whether induced shifts in remembered spatial frequency are also tuned for orientation. Earlier studies using the memory masking paradigm have demonstrated that changes in the orientation of the masking stimulus have no effect on spatial frequency discrimination thresholds (Magnussen et al., 1991) and indicate that memory masking occurs only for relevant stimulus attributes (Magnussen & Greenlee, 1999). In Fig. 8 results are shown for an experiment in which the orientation of masking stimuli were systematically varied and the effects on PSEs were measured for the non-coincident version of the delayed spatial frequency discrimination task. The spatial frequency of the reference stimulus was 3 c/deg and masks of 1.5, 3 and 6 c/deg were presented with orientation shifts relative to the reference stimuli that varied between 0 deg and 90 deg in a counter-clockwise direction. As can be observed mask orientation appears to have little or no effect on the induced shifts in matched spatial frequency. The effective masks (6 and 1.5 c/deg) induce respective shifts that are above and below baseline performance for all orientations. The ineffective mask (3 c/deg) continues to have little effect of PSE regardless of its orientation, consistent with previous findings (Magnussen et al., 1991).

4. Discussion

The purpose of this paper was to investigate the proposed links between visual sensory processing and visual perceptual memory. Using a delayed spatial frequency discrimination task we assessed the extent to which information that is retained about the spatial frequency of a visual stimulus is vulnerable to disruption by the presentation of interfering stimuli during the inter-stimulus interval. Using this 'memory masking' paradigm we were able to measure the accuracy with which visual stimuli were retained by perceptual memory mechanisms and assess the effects that the interfering stimuli had on the fidelity of that memory store. Our central finding is that masking stimuli are able to shift PSE for matches made by observers between the remembered reference and test stimuli, as long as their spatial frequency is within a bandwidth of approximately 1.2 octaves of the reference spatial frequency. When mask spatial frequencies differ by more than this value, there is little or no change in PSE from baseline (no masking) levels. This selective pattern of masking is observed for reference stimuli of different spatial frequencies and points to the existence of multiple, spatially tuned mechanisms in visual perceptual memory similar to those which operate as part of the basic sensory analysis of spatial information.

4.1. Visual perceptual memory and low-level visual processing

The existence of multiple spatially tuned mechanisms in low-level perceptual memory is in accord with those models which

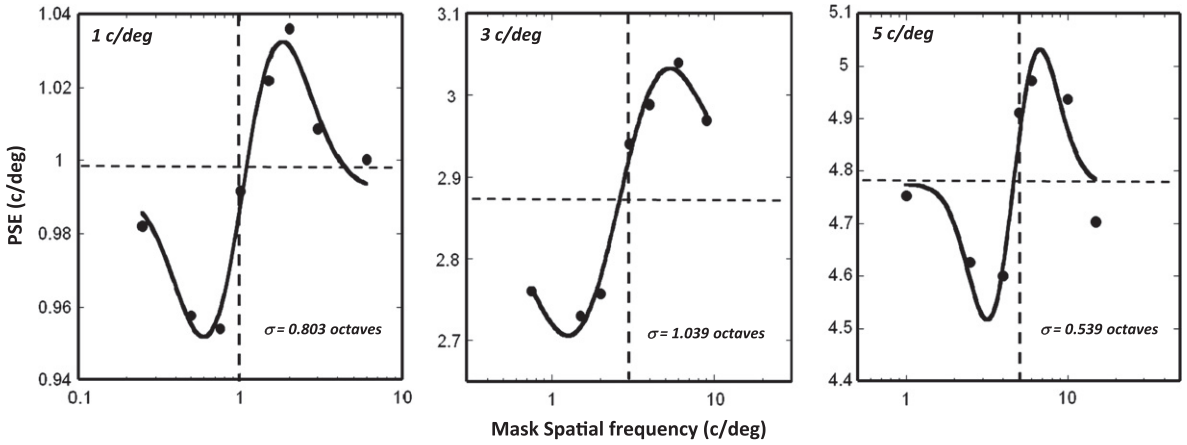

Fig. 4. Variation in PSE as a function of mask spatial frequency for three different reference spatial frequencies (1, 3 and 5 c/deg). The data in each case represent the average of three observers and have been fitted by a first derivative of a Gaussian function similar to the data in Fig. 3.

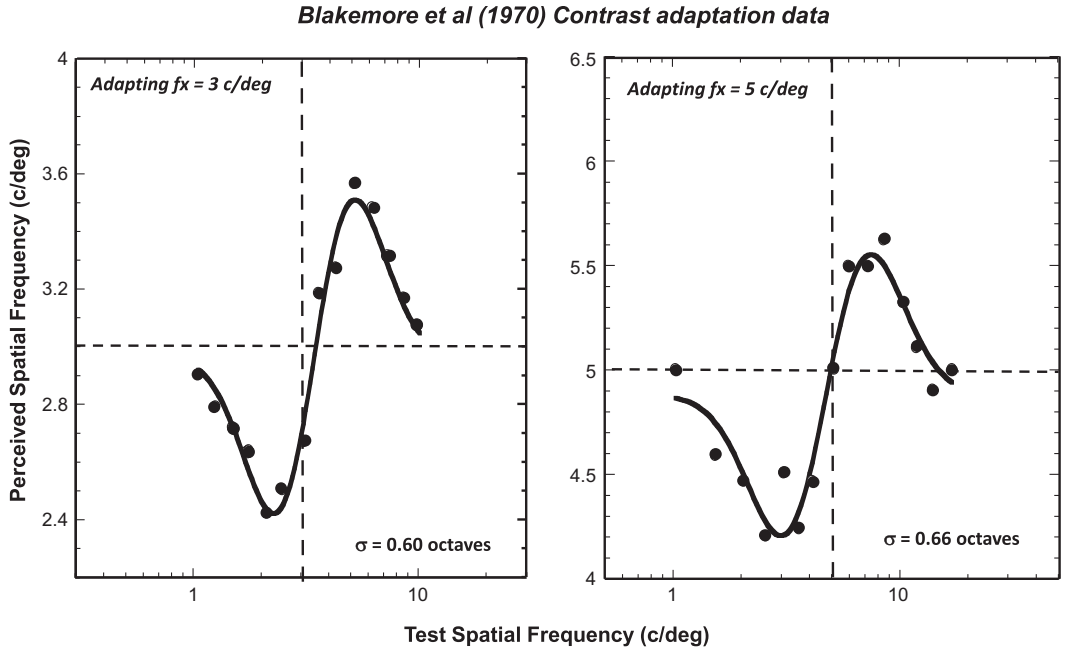

Fig. 5. Contrast adaptation data from Blakemore, Nachmias, and Sutton (1970) which plot the variation in perceived spatial frequency of test stimuli following prior adaptation to a 3 c/deg (A) and a 5 c/deg (B) grating stimulus. The data, similar to the memory masking data shown in Figs. 3 and 4, have been fitted by a first derivative of a Gaussian function.

describe perceptual memory as comprising an array of stores that are able to retain information about a particular stimulus dimension within only a limited range or bandwidth (Magnussen, 2000, 2009; Magnussen & Greenlee, 1999; Magnussen et al., 1991). The masking bandwidths we have measured for different reference spatial frequencies range between 0.54 and 1.04 octaves for the spatially co-incident versions of the task and between 0.86 and 1.15 octaves for the non-coincident versions. These bandwidth measures are in good agreement with those obtained from adaptation and traditional sensory masking paradigms (e.g. Georgeson, 1980; Greenlee & Magnussen, 1988; Wilson, McFarlane, & Philips, 1983) which in turn are similar to those that have been measured in primate V1 neurons. DeValois, Albrecht, and Thorell (1982) for example, have shown that the bandwidth range for macaque foveal V1 neurons is between 0.7 and 2.5 octaves. The consistency between the tuning bandwidths displayed by perceptual memory mechanisms and visual neurons in V1 implies that the former are closely linked to sensory discrimination properties of the latter (Magnussen, 2009). Thus, it would appear that the neural mechanisms that serve to retain spatial frequency information in perceptual memory adhere to similar organisational principles to those exhibited by the sensory channels/filters that are involved in the earliest visual analysis of this information. In this respect, the data presented here further strengthen the links that are increasingly being drawn between mechanisms that underpin basic visual sensory processing and those which are involved in the short term retention of this information (Pasternak & Greenlee, 2005).

Results from contrast adaptation experiments have made fundamental contributions to the elucidation of the organisation of low-level sensory processing of spatial frequency information in the primate visual system (Bjørklund & Magnussen, 1981; Blakemore & Campbell, 1969; Georgeson & Harris, 1984). Whilst perceptual memory mechanisms appear to share common properties with basic sensory processing, it is important to note that there

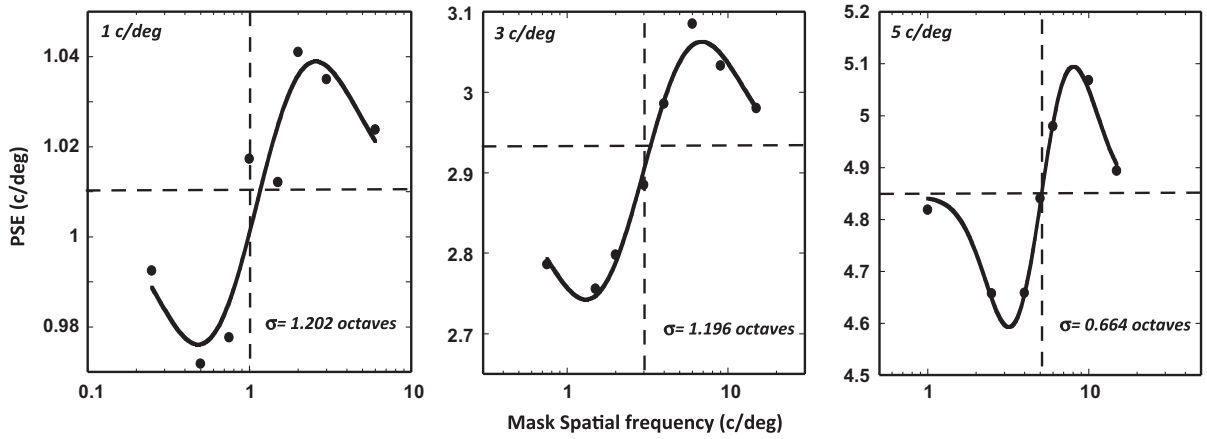

Fig. 6. The variation in PSE as a function of mask spatial frequency for the spatially non-coincident version of the task. In this version of the experiment the centres of the reference, mask and test stimulus were horizontally separated from each other by 3 deg. The data in each case represent the average of 3 observers and have been fitted by functions similar to those in previous figures.

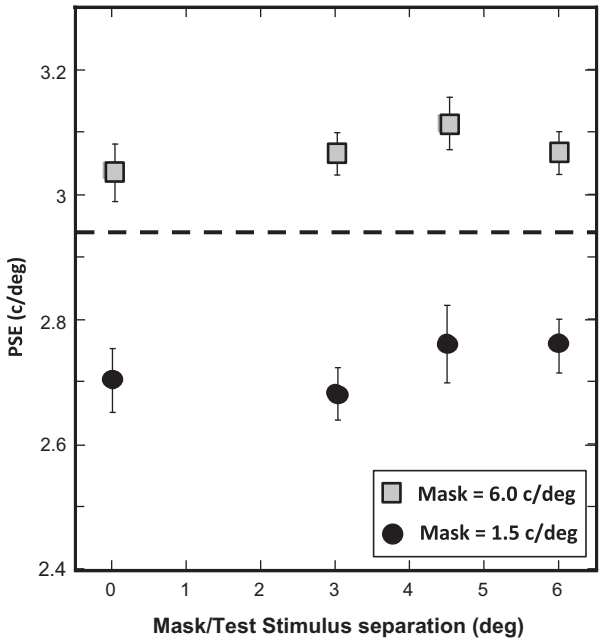

Fig. 7. Shifts in PSE for spatial frequency matches made for a 3 c/deg reference stimulus with masking stimuli (6 and 1.5 c/deg) placed at increasing larger horizontal separations. The results represent the average data from three observers.

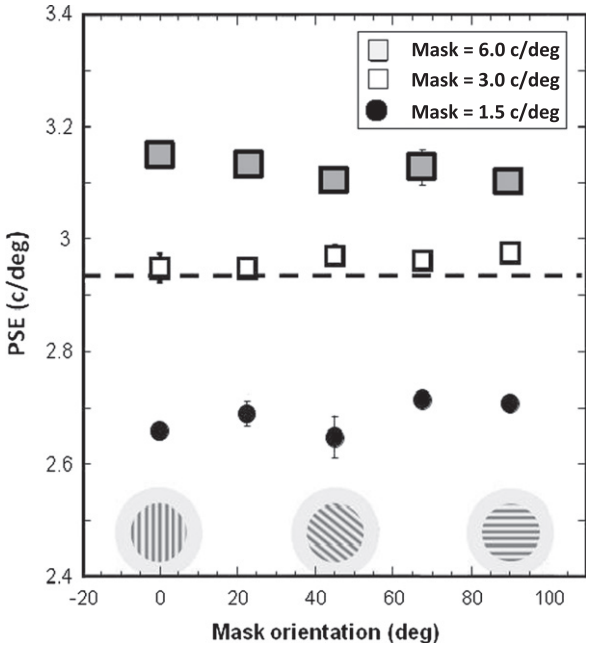

Fig. 8. Shifts in PSE for spatial frequency matches made for a 3 c/deg reference stimulus with masking stimuli (6 and 1.5 c/deg) at different orientations relative to the reference.

are differences between results that have emerged from contrast adaptation and memory masking experiments. These may serve to highlight the fact that the neural processes that underpin sensory and perceptual memory mechanisms are not completely overlapping. One such difference lies in the fact that the retention of spatial frequency information in perceptual memory lacks orientation selectivity (Regan, 1985). For perceptual memory mechanisms an effective masking stimulus remains effective regardless of its orientation (Magnussen, Greenlee, & Thomas, 1996). This is in stark comparison to contrast adaptation experiments (e.g. Blakemore & Nachmias, 1971; Blakemore, Nachmias, & Sutton, 1970) which have clearly shown that the effects of adapting to a luminance contrast grating are highly orientation dependent and are abolished if the adapt and test grating differ by more than 40 deg (Movshon & Blakemore, 1973). This study also demonstrates that the interference effects induced by memory masking stimuli have a much broader spatial extent across the retina compared to those induced by contrast adaptation. Previous psychophysical studies have shown that the effects of contrast adaptation are greatest when the adapting and test stimuli are spatially coincident, but rapidly decrease when their separation increases (Ejima & Takahashi, 1984, 1985; Williams, Wilson, & Cowan, 1982). Memory masking for spatial frequency, on the other hand, still occurs for effective mask stimuli, with little decrease in magnitude, at horizontal separations of up to 6 deg – a distance well outside that measured for contrast adaptation effects (Ejima & Takahashi, 1984). These spatially long range effects are at odds with single-unit, behavioural and neuroimaging experiments which have shown that the short term retention of visual information is highly spatially localised (Hollingworth, 2006, 2007; Sneve et al., 2011; Zaksas, Bisley, & Pasternak, 2001). However, they are consistent with other studies which suggest the existence of a more spatially global mechanism that retains sensory information from across the visual field (Ester, Serences, & Awh, 2009). In addition,

psychophysical results obtained by Tanaka and Sagi (1998b), also indicate the presence of spatially long-range and long-lasting facilitation effects in the detection of Gabor contrast patterns. Tanaka and Sagi's work highlights the fact that low-level spatial filters do have the capability to retain information about visually presented patterns far beyond their normal limits of spatial and temporal integration. These properties may form the basis for the storage of spatial information in memory (Tanaka & Sagi, 1998a, 1998b). Nonetheless, the fact that the effects mediated by perceptual memory mechanisms appear to have a much broader range of transfer across space and orientation compared to those mediated directly by low-level sensory mechanisms, suggests they are likely to be supported by neural processing at a level beyond V1 where neurons have the ability to integrate across different stimulus attributes (DeValois & DeValois, 1990). In this respect the effects of memory masking have similar properties to more complex after-effects, such as the gender specific face after-effect, which are considered to be mediated by high level visual areas (Afraz & Cavanagh, 2009). Furthermore, the fact that memory masking has been shown to be dependent upon distal as opposed to retinal spatial frequency (Bennett & Cortese, 1996) also points to the fact that perceptual memory operates at a level beyond V1 where size and shape constancies are computed.

4.2. Visual perceptual memory and visual short term memory

A characteristic property of visual information that is retained within low-level perceptual memory is that it is malleable and vulnerable to interference. This suggests that there may be some overlap with a weak or fragile form of visual short term memory (VSTM), the existence of which has been mooted by certain studies (e.g. Sligte, Scholte, & Lamme, 2008, 2009). These studies form part of a wider body of work which describes the transfer of low-level sensory information into memory as a multi-stage process (Lalonde & Chaudhuri, 2002; Magnussen, Idas, & Holst-Myhre, 1998; Sligte, Scholte, & Lamme, 2008, 2009; Tanaka & Sagi, 2000). Within this process the weak form of VSTM operates for temporal durations of the order of around 4 s or less (Lalonde & Chaudhuri, 2002; Magnussen, Idas, & Holst-Myhre, 1998), is closely allied to low-level sensory processing and is vulnerable to interference. Currently, it is an open question as to whether this more volatile or fragile form of VSTM actually constitutes part of a continuum with iconic visual memory, or is in fact a distinct and separate process in itself (Sligte, Scholte, & Lamme, 2009). Regardless of this issue, the properties of volatile VSTM have much in common with the characteristics of low-level perceptual memory revealed in this study and in all likelihood constitute similar mechanisms. For longer durations a stronger and more robust form of VSTM is proposed to exist which is characterised as having a limited storage capacity but is less vulnerable to interference (Luck & Vogel, 1997; Sligte, Scholte, & Lamme, 2008, 2009). A key feature of this robust form of VSTM, which further differentiates it from the more volatile form of VSTM, is that it appears to be under the control of attention which gates low-level visual signals as part of the generation of more long term memory representations (Lalonde & Chaudhuri, 2002; Tanaka & Sagi, 2000). Recent brain imaging studies have shown that the neural activity that accompanies VSTM is distinct from that which accompanies attention and lies outside the early visual areas (Offen, Schluppeck, & Heeger, 2009). The extent of activation of area V4, in particular, may provide an index as to the degree to which the representation in VSTM is vulnerable to interference (Sligte, Scholte, & Lamme, 2009).

In conclusion, this study demonstrates that the mechanisms that underpin the short term retention of information about spatial frequency in perceptual memory are tuned in a similar manner to the channels or filters that operate right from the earliest levels of low-level spatial processing. This further emphasises the link between memory mechanisms and basic sensory processing mechanisms that are being used as a basis for the retention of information. However, whilst certain characteristics of perceptual memory are highly consistent with the kind of analysis that occurs in the earliest stages of visual processing, the broad transfer properties of memory masking across location and orientation for example, suggest more complex interactions. Such interactions are likely to involve visual areas beyond the primary visual cortex. In this and other respects, low-level perceptual memory shares common properties with the more volatile forms of VSTM that have been described previously.

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The Retention and Disruption of Colour Information in Human Visual Perceptual Memory.

Running title: Perceptual Memory for Colour

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Abstract

Previous studies have demonstrated that the retention of information in short term visual perceptual memory can be disrupted by the presentation of masking stimuli during inter-stimulus intervals (ISIs) in delayed discrimination tasks. We have exploited this effect in order to determine to what extent short term perceptual memory is selective for stimulus colour. We employed a delayed hue discrimination paradigm to measure the fidelity with which colour information was retained in short term memory. The task required 5 colour normal observers to discriminate between spatially non-overlapping coloured reference and test stimuli which were temporally separated by an ISI of 5s. The points of subjective equality (PSEs) on the resultant psychometric matching functions provided an index of performance. Measurements were made in the presence and absence of mask stimuli presented during the ISI which varied in hue around the equiluminant plane in DKL colour space. For all reference stimuli we found a consistent mask-induced, hue-dependent shift in PSE compared to the 'no mask' conditions. These shifts were found to be tuned in colour space, only occurring for a range of mask hues that fell within bandwidths of 29 – 37 deg. Outside of this range, masking stimuli had little or no effect on measured PSEs. The results demonstrate that memory masking for colour exhibits selectivity similar to that which has already been demonstrated for other visual attributes. The relatively narrow tuning of these interference effects suggests that short term perceptual memory for colour is based upon higher order, non-linear colour coding.

Keywords: colour, visual perceptual memory.

Introduction

The ability of the brain to store sensory information in short-term memory provides an important means by which detail about the surrounding environment can be retained and subsequently used to mediate or direct behaviour (Baddeley, 1986). This link between perception and memory has been further emphasised by studies which have highlighted the close association that exists between the neural mechanisms that mediate the storage of sensory information in short term memory and those involved in its sensory encoding (Gibson & Maunsell, 1997; Fuster, 1997; Bisley & Pasternak, 2000; Pasternak & Greenlee, 2005; Graham, Barense & Lee, 2010; Kang et al., 2011). This association has been most clearly articulated for our visual sense, where the retention of information relating to different attributes of visual stimuli has been proposed to occur within what has been termed 'low-level perceptual memory' (Magnussen & Greenlee, 1999; Magnussen, 2009). This form of memory is described as operating in a non-declarative, implicit fashion and constitutes a pre-semantic level of storage for low-level sensory information (Magnussen, 2000; 2009). Low-level visual perceptual memory is thought to be based upon neural activity that takes place within a network of brain areas distributed throughout the cerebral cortex that are located beyond V1, but early in the cortical processing stream (Fuster, 1997; Offen et al., 2009; Magnussen, 2009). Related concepts include sensory working memory (Pasternak & Greenlee, 2005), the perceptual representation system (Schacter et al., 2000) and weak or fragile forms of visual short term memory (Sligte et al., 2008; 2009).

The short term storage of visual information has been studied in detail at both behavioural and single neuronal levels (Regan, 1985; Miyashita & Chang, 1988; Magnussen & Greenlee, 1992; 1999; Magnussen et al. 1991; 1996; Bisley & Pasternak, 2000; Bisley, Zaksas & Pasternak, 2001;

Zaksas, Bisley & Pasternak, 2001; Pasternak & Zaksas, 2003; Bisley, Zaksas, Droll & Pasternak, 2004). What is apparent from these studies is that short term perceptual memory is dimension or feature specific, i.e. there appears to be a series of parallel mechanisms linked to memory formation that are devoted to particular attributes of a visual stimulus, such as its contrast, spatial frequency or motion (Magnussen & Greenlee, 1999; Magnussen, 2000; Pasternak & Greenlee; 2005). Such feature specificity has been demonstrated by 'dual-task' experiments where observers have to retain information and make subsequent judgements about two stimulus features. This can be done for different attributes (e.g. contrast and spatial frequency) virtually without impairment. However, when observers are asked to make judgements about the same feature (e.g. two spatial frequencies), thresholds are significantly elevated (Magnussen et al., 1991; Magnussen & Greenlee, 1999). Feature specificity in short term perceptual memory has also been demonstrated by the effects of interference or masking stimuli presented during the *ISIs* of delayed discrimination tasks (Magnussen et al., 1991; Magnussen & Greenlee, 1992, McKeefry et al., 2007; Bennett & Cortese, 1996). These so called 'memory masking' effects are outside the temporal range of those that are normally associated with traditional sensory masking paradigms (Breitmeyer, 1984). Experiments like these highlight the fact that sensory information that is retained by short term visual perceptual memory is vulnerable to disruption or disturbance by subsequently presented visual stimuli. Crucially, this disruption occurs only for certain relevant features of the mask stimulus. Moreover, the effects are tuned, occurring only across narrow ranges of these features (Magnussen et al., 1991; Magnussen & Greenlee, 1992; Lalonde & Chaudhuri, 2002; McKeefry et al., 2007). These selective effects have been interpreted as revealing a modular organisation of visual short term memory which is purported to consist of an array of parallel stores, each tuned to a relatively narrow range of stimulus parameters, which are linked in a lateral

inhibitory network, where interference occurs within but not between stores (Magnussen, 2000).

Colour forms another important feature of our visual environment from which information can be extracted. The sensory analysis of colour is based upon anatomically segregated and physiologically distinct processing pathways (see: Gegenfurtner, 2003; Solomon & Lennie, 2007 for reviews). Sub-cortical colour processing is based upon outputs from L- (long), M-(middle) and S-(short) wavelength sensitive cones which interact in a linear fashion to form 'red-green' (L-M) and 'blue-yellow' (S-(L+M)) opponent mechanisms. This cone-opponent model of organisation has satisfactorily accounted for many aspects of colour perception (DeValois et al., 1966; Derrington et al., 1984; Mullen & Losada, 1994). However, within the visual cortex the neural processing of colour appears to undergo a transformation. Numerous experimental observations, both behavioural and neurophysiological, point to the existence of more than two chromatic mechanisms with spectral sensitivities that are very different from the cone-opponent channels (Krauskopf et al., 1986; Webster & Mollon, 1991; DeValois et al., 1997; Lennie et al., 1990; Zaidi & Halevy, 1993; Li & Lennie, 1997; Goda & Fuji, 2001: DeValois et al. 2000b; Conway, 2003; Clifford et al, 2003; McGraw et al., 2004; Xiao *et al.*, 2007, see: Eskew, 2009 for a review). One important difference is that these so-called 'higher-order' chromatic mechanisms have been shown to have narrower spectral tuning characteristics (Goda & Fuji, 2001; DeValois et al. 2000b; McKeefry et al. 2004; but see: D'Zmura & Knoblauch 1997 for a counterview), a property which can only arise as a result of non-linear combinations of cone inputs (DeValois et al., 2000a,b). This property further differentiates them from cone-opponent mechanisms which are based upon linear combinations of cone inputs and are more spectrally broadband (Derrington et al., 1984; DeValois et al., 2000a).

Up to now there has been little attempt to try and examine short term memory for colour in the context of the underlying sensory physiology described above. This approach seems particularly pertinent in view of the recent emphasis on the close links between the neural mechanisms that underlie the analysis of sensory information and those involved in its retention in short term memory (Pasternak & Greenlee, 2005). The aim of these experiments was to examine the extent to which perceptual memory displays selectivity for stimulus colour. We used a memory masking paradigm in order to assess how the chromaticity of a masking stimulus determines the extent to which it can interfere with the fidelity of a stored representation of a coloured reference stimulus. This paradigm has been successful in revealing the spatial tuning and speed selectivity of perceptual memory in previous experiments (Magnussen & Greenlee, 1992; Magnussen et al., 1991; McKeefry et al., 2007). There are two key questions we want to address: firstly, do parallel stores for stimulus colour exist in short term perceptual memory, similar to those which have been shown for spatial frequency and speed? Secondly, if memory masking experiments do reveal some form of colour selectivity, can this tell us anything about how colour information is organised in short term perceptual memory? For example, is colour information retained by mechanisms that are based upon linear, broadband cone-opponent processing or instead stored by non-linear, narrowband, higher order colour processing mechanisms in the brain?

Methods

Stimuli

The colour stimuli used in these experiments consisted of hard edged circular coloured patches which subtended 1.5° and were presented on a uniform grey background of the same mean luminance (12.5cd/m^2). The stimuli were generated using purpose built software which drove a video graphics card (VSG 2/5; Cambridge Research Systems, Rochester, UK) and were displayed on a high resolution colour graphics monitor (GDM520, Sony, Tokyo, Japan, frame rate 120 Hz) which subtended 26.3° x 32.75°. In the main experiments the chromaticities of the colour stimuli were specified as equal length vectors in *DKL* colour space (Derrington, Krauskopf & Lennie, 1984) which were defined by their angle of rotation (ϕ) in the isoluminant plane (see figure 1). The endpoints of these vectors formed a circle around illuminant C (CIE 1931 chromaticity co-ordinates; x = 0.310, y = 0.316). Monitor calibration was performed by using a ColourCal probe (Cambridge Research Systems Ltd., Rochester, UK) and with a PR-650 Spectrascan SpectraColorimeter (Photoresearch, Chatsworth, California, USA). In additional experiments the luminance contrast content of the mask stimuli was varied via manipulation of their luminance ratio (*LR*) defined as:

$$LR = \frac{L_{ms}}{L_{ms}+L_{bkgrd}} \quad (1)$$

where; L_{ms} = luminance of masking stimulus and L_{bkgrd} = luminance of background. An *LR* = 0.5 generates a mask stimulus that is photometrically equiluminant with the background (i.e. contains only chromatic contrast). Values either side of this generate stimuli containing varying amounts of luminance and chromatic contrast, with luminance increments denoted by *LR*>0.5 and decrements by *LR*<0.5.

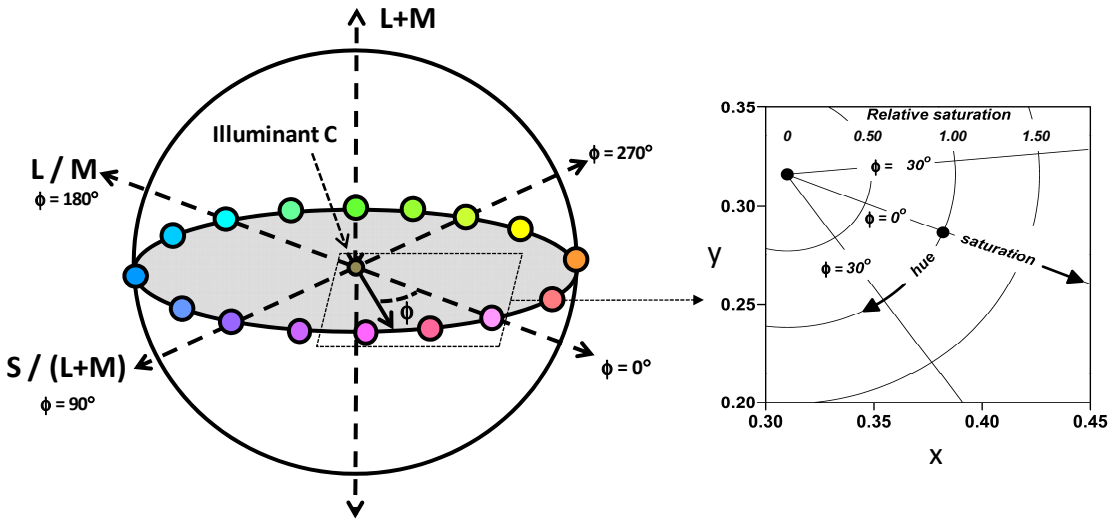

Figure 1. Specification of colour stimuli used in the experiments. The left hand panel shows DKL colour space which was used to specify the chromatic stimuli used in these experiments. Stimuli were generated by equal length vectors in this space and were sampled around the equiluminant plane with their hue being defined by the angle of rotation (ϕ). Illuminant C (CIE 1931 x = 0.310, y = 0.316) formed the centre of this colour space. The right hand panel illustrates an enlarged section of the chromaticity diagram to show the direction of movement through colour space when hue and saturation are altered. The concentric circles indicate the baseline saturation of unity together with higher and lower saturations (1.5 and 0.5). Saturation of the stimulus could be changed by increasing the vector length in the direction shown.

Four main reference stimuli were used in this set of experiments which were reported by the individual observers as being exemplars of four main colour categories red, green, blue and yellow, i.e. unique hues. These stimuli were specified by preliminary experiments where observers performed a hue scaling procedure in order to determine their location in *DKL* colour space. A 4-alternative-forced-response procedure was used where they indicated whether presented colour stimuli appeared blue, green, yellow or red (DeValois et al., 1997; Parry et al. 2006). We presented 20 different chromatic axes which represented vectors that were equally spaced in steps of 18° ranging from ϕ=0° to ϕ=360° around illuminant C. The results were analyzed by deriving four colour naming functions *p*[red], *p*[blue], *p*[green] and *p*[yellow], where *p*[colour] was the proportion of times that a particular test hue was called that colour out of a total of 20 presentations. The exemplars of four main hues (red, blue, green, and

yellow) were defined as the central maxima of the hue scaling functions. In control experiments we also used reference stimuli that were equally likely to be classified into adjacent colour categories, rather than unique or exemplar hues. Results obtained with these 'non-unique' stimuli were similar to those obtained with the standard reference stimuli.

Procedure

In the main experiments a delayed colour discrimination paradigm was used to measure the fidelity of stored colour information in perceptual memory. The paradigm employed a 2-alternative-forced-choice procedure in conjunction with a method of constant stimuli. Each trial began with the presentation of a reference stimulus of 380 ms duration; this was followed by a 5 s ISI and in the middle of this period a mask stimulus of variable chromaticity was presented for 2 s. At the end of the *ISI* a test stimulus was presented for 380 ms (see figure 2). The reference, mask and test stimuli were separated horizontally to avoid retinal adaptation effects. The reference was presented 3° to the right of the fixation point, the mask stimulus was centred on the fixation point and the test was presented 3° to the left of fixation. The test stimulus could be one of seven colours which sampled equally (in terms of ϕ) across a range of hues on the isoluminant colour circle either side of the reference stimulus colour. The range of test stimuli used was determined in preliminary experiments so that the two endpoint colours were those hues closest to the reference stimuli that were 100% discriminable from it. This ensured that the test and reference stimuli fell within the same colour categories rendering any attempt by observers to employ verbal, colour naming strategies ineffective for task performance.

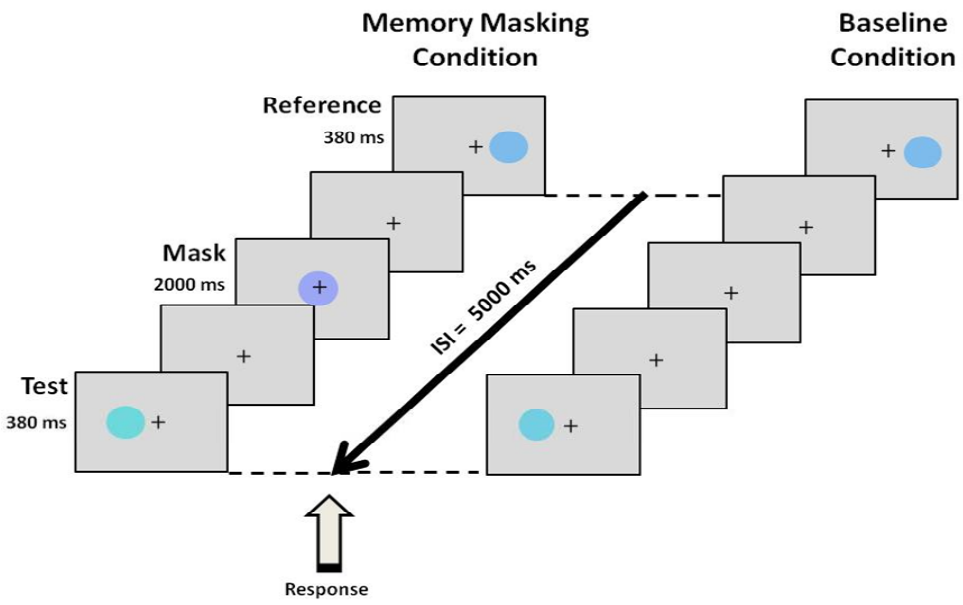

Figure 2. Schematic representation of the delayed colour discrimination task. In the baseline condition a reference stimulus appeared 3° to the right of a central fixation cross for 380 ms. Following an inter-stimulus interval (ISI) of 5s, a test stimulus appeared 3° to the left of the fixation mark also for 380 ms. Observers were requested to indicate, via a button press, how they perceived the colour of the test relative to the reference (see text). In the memory masking condition the paradigm was identical except that an additional mask stimulus appeared for 2s during the ISI, appearing in the centre of the screen coincident with the fixation point. All colour stimuli subtended 1.5°.

Following the end of each trial the observers were instructed to respond by button press (CB3 response box; Cambridge Research Systems) to indicate where they considered the test stimulus hue to be located on the colour circle relative to that of the remembered reference colour. In practice, this meant that for a blue reference stimulus, for example, observers were instructed to indicate whether the test stimulus appeared to be more 'green' or 'purple'; for a red stimulus the response was whether the test was more 'purple' or 'orange' and so forth for each of the reference colour stimuli used. This procedure enabled us to plot psychometric functions which then allowed us to assess the effects of different mask stimuli on performance, in particular the extent to which mask stimuli affected the point of subjective equality (*PSE*) between the test and remembered reference colours. Performance on the delayed colour discrimination paradigm was assessed relative to performance on the baseline condition, where

no mask stimulus was introduced during the ISI. Each psychometric curve was based upon a minimum of 140 trials which were randomly interleaved across four 1 hour sessions. This randomised presentation was adopted in order to prevent the build up of more long term representations in memory of the stimuli.

Data analysis

The psychometric data were fitted by a logistic function of the form:

$$y = \frac{100}{\left(1 + e^{\frac{(\phi - \mu)}{\theta}}\right)} \quad (2)$$

where; y is the percentage of times the test stimulus was reported as being rotated in an anticlockwise rotation in colour space relative to the reference, ϕ is the chromatic axis of the test stimulus, μ is the relative rotation in colour space corresponding to the 50% level on the psychometric function (i.e. the point of subjective equality (PSE)) and θ is an estimate of the colour discrimination threshold.

The PSE data were plotted as a function of mask chromatic axis and fitted by a first derivative of a Gaussian function described by the equation:

$$y = y_{pos} + \left[\left(\frac{A}{(\sigma . e^{-0.5})}\right) * \left(\phi - x_{pos}\right) * e^{-\left(\frac{\left(\phi - x_{pos}\right)^2}{2\sigma^2}\right)}\right] \quad (3)$$

where; y is the point of subjective equality (PSE), ϕ is the chromatic axis of the mask in DKL colour space, σ is the standard deviation of the Gaussian, A is the half-amplitude of the function and x_{pos}, y_{pos} is the origin of the function (when $\phi = x_{pos}$, PSE = y_{pos}). The half amplitude of this function represents the magnitude by which the PSE deviates from baseline. The maxima and

minima of this function occur at mask chromatic axis orientations +/-σ units from the origin (i.e. $(\phi - x_{pos}) = +/-\sigma$).

Observers

Five observers took part in the study (3 females and 2 males; mean age = 36.2 years, s.d.= +/-5.6 years), two of whom were authors, the remaining three were naive as to the aims of the experiment. All gave informed consent and had normal colour vision according to Rayleigh matches made on a HMC Anomaloskop and the Farnsworth-Munsell 100-Hue test. All had 6/6 or corrected to 6/6 Snellen visual acuity. The experiments were performed in a darkened room and observers fixated on a small black cross on the centre of the screen which was viewed binocularly from a distance of 114 cm.

Results

Figure 3 shows representative individual data obtained from the memory masking experiments for each of the four main reference colour stimuli (red, green blue and yellow). The graphs plot how *PSEs* vary as a function of mask stimulus chromatic axis (ϕ) and are specified in terms of the rotation of the chromatic axis in *DKL* colour space of the matched test stimulus relative to the reference stimulus. As can be seen in the plots the colour matches made by the observers are highly dependent upon the chromaticity of the masking stimulus and a similar pattern can be observed regardless of the colour of the reference stimulus. When mask colour is identical to the reference (i.e. zero relative rotation) the resultant *PSEs* are similar to those obtained for the baseline (no mask) conditions (horizontal dashed lines). However, when the chromatic axis of the mask stimulus shifts away from that of the reference there are small but systematic variations in the *PSE* away from baseline levels. For example, when the mask axis rotates in a clockwise direction in colour space (positive relative rotation) the matches made by the observers are shifted away from the baseline value towards the hue of the mask stimulus. The deviation from baseline reaches a maximum with increasing rotation but then starts to decrease and approach baseline levels as mask chromaticity shifts even further away from that of the reference. When the mask chromatic axis rotates away from the reference in an anti-clockwise direction (negative relative rotations) the *PSEs* are shifted in the opposite direction, reaching a maximum then returning to baseline.

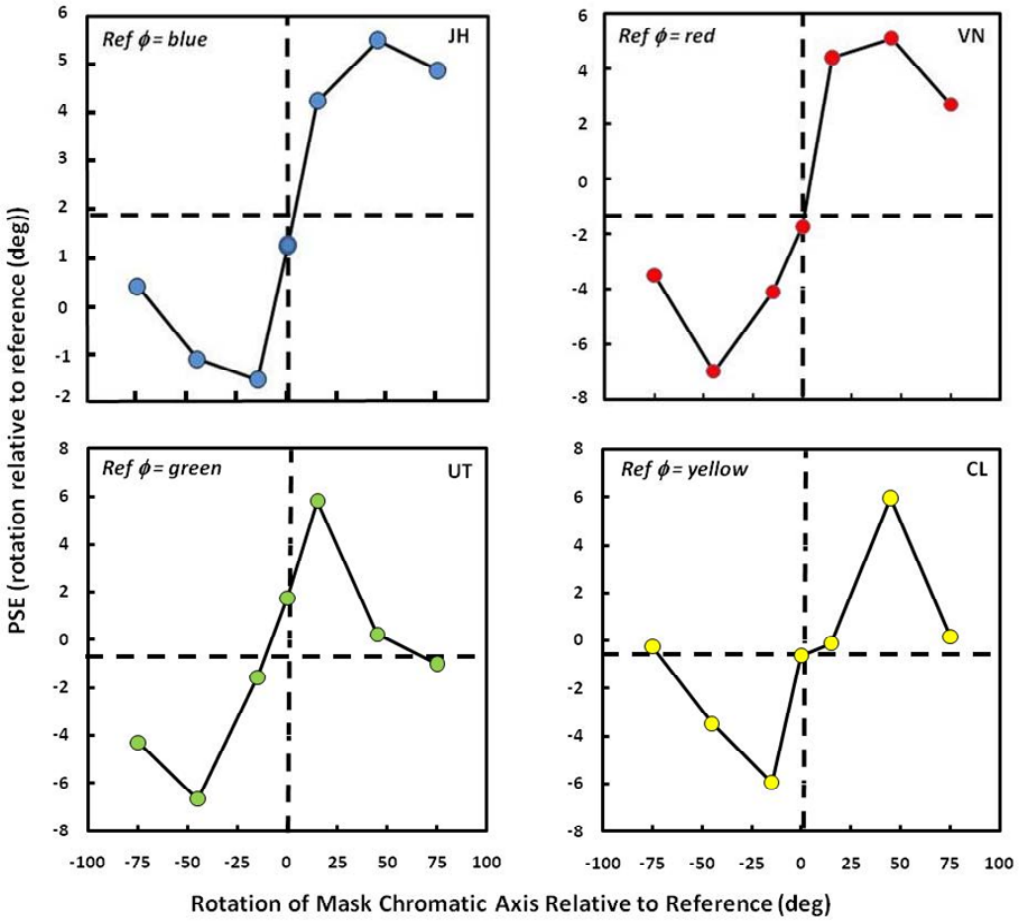

Figure 3. Data from the colour memory masking experiment. Representative results are shown for single observers for four reference colours (blue (ϕ = 126°), red (ϕ = 18°), green (ϕ = 216°) and yellow (ϕ = 288°)). PSEs obtained from the psychometric curve fits are plotted as a function of rotation of mask chromatic axis relative to the reference in colour space. The horizontal dashed lines indicate baseline (i.e. no mask) performance and the vertical dashed lines indicate conditions where the reference and the mask stimuli have the same chromatic axis.

The pattern of these results suggests that the mask stimulus can interfere with the stored representation of the colour of the reference stimulus and can induce a shift in the point of perceived equality as long the mask colour is different, but not too different, from the reference stimulus. Thus it would appear that memory masking for colour exhibits tuning or selectivity similar to that which has already been demonstrated for other visual attributes such as motion and spatial frequency (Magnussen et al., 1991, McKeefry et al., 2007). In order to ensure that these masking effects are indeed localised to a specific region of colour space we

performed an additional experiment on two subjects in which delayed colour matching was measured in the presence of mask stimuli sampled from across the full 360° of the DKL colour circle. The results from this experiment are shown in figure 4 where the effects of masking can be seen to occur only within a narrow range centred on the reference stimulus (blue ϕ = 120°).

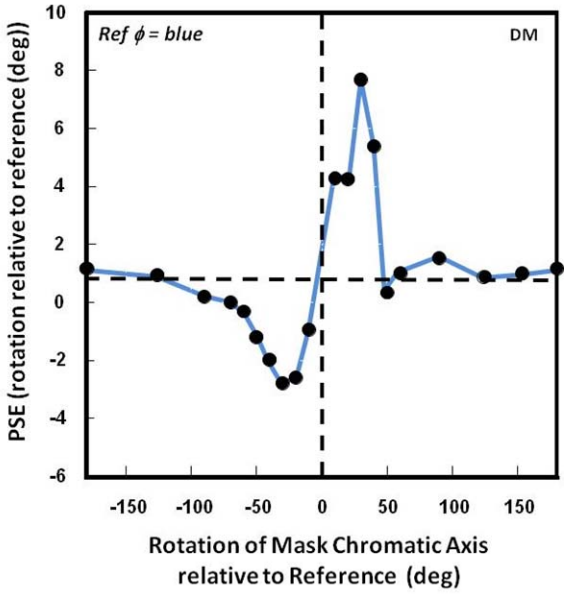

Figure 4. Data from a control experiment where mask stimuli were sampled from across the full 360° of DKL colour space. In this example the reference stimulus was blue (ϕ = 126°) and the results are for a single observer (DM).

The tuned nature of these masking effects prompted us to fit the data with first derivative of Gaussian functions which allowed us to derive an estimate for the bandwidth (σ) of these tuning functions (see methods). The results of this procedure are shown in figure 5 where the group averaged data (n=5) for each reference stimulus have been fitted by these functions. The resulting values for the bandwidths of the masking effects were: 36.8° for the blue reference stimulus, 33.4° for the green, 29.1° for the yellow and 34.1° for the red.

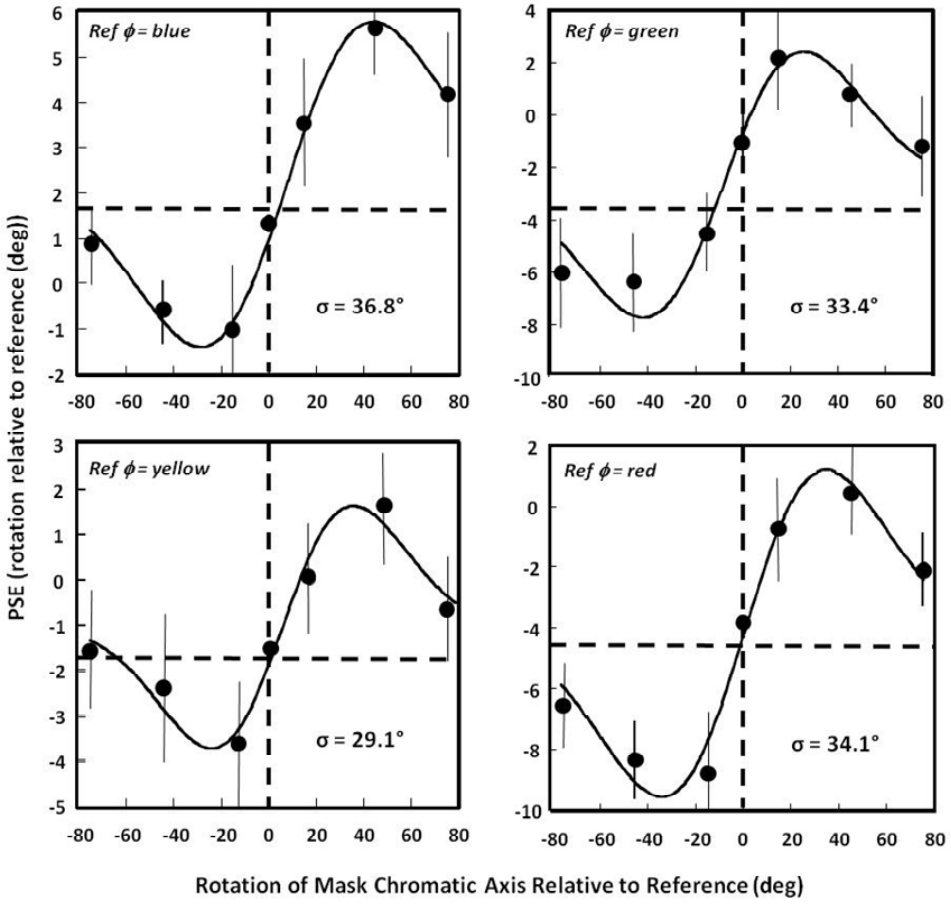

Figure 5. Group averaged memory masking data (n = 5) for the four main reference stimuli. The data have been fitted with the 1st derivative of a Gaussian function (see methods). From this fitting procedure the value, σ provides an estimate of bandwidth in DKL colour space across which masking stimuli are effective in interfering with the retention of the chromatic stimulus in short term perceptual memory. Error bars represent +/- 1 s.d. of the mean.

Implicit in our stimulus design is the assumption that equal length vectors in DKL colour space generate stimuli which have the same perceived saturation (see figure 1B). This is not a valid assumption in view of the perceptual non-uniformity of this colour space. In order to demonstrate that these colour memory masking effects were not simply the result of differences in perceived saturation of the masking stimuli, we examined the effects of varying their saturation. This was achieved by varying the vector length in colour space and was expressed relative to the standard condition (see figure 1B). We chose two masking stimuli; one

was an effective mask, i.e. a mask stimulus that induced a shift in PSE away from baseline performance. The other, was an ineffective mask defined by a chromatic axis that lay well outside the region of colour space where it had any measureable effect on the PSE obtained for the chosen reference colour. Figure 6 shows results from 2 observers who performed this experiment. The reference stimulus in this case was an exemplar of the red colour category and the effective mask had a chromatic axis (ϕ) which was rotated 34° clockwise in colour space relative to the reference. The ineffective mask had a chromatic axis rotated 108° clockwise, relative to the reference. As can be observed, ineffective masks have minimal effect on the PSE obtained from the delayed discrimination experiments and this is the case regardless of their saturation. An ineffective mask cannot be made effective simply by increasing its saturation. By comparison, over the same range an effective mask generated increasingly larger shifts in PSE with increasing saturation.

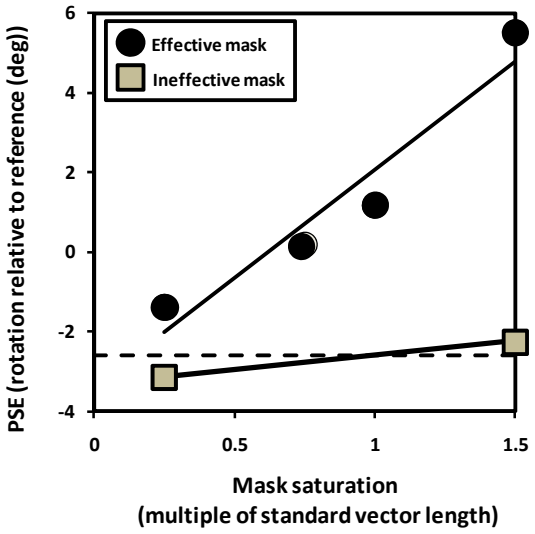

Figure 6. PSE values plotted as a function of mask saturation levels. The graphs plot how PSEs for a red reference stimulus (ϕ = 18°) are shifted for effective masks ((ϕ = 34°) of increasing saturation and ineffective masks (ϕ = 108°). The data represent the average performance of 2 observers and have been fitted by linear regression lines. The horizontal dashed line indicates baseline (no-mask) performance.

A key property of visual perceptual memory is that it is attribute or dimension specific (Magnussen, 2009). This has been demonstrated in memory masking experiments by the fact that masking only occurs for certain relevant parameters (Magnussen & Greenlee, 1999). We wanted to examine in an analogous fashion to what extent the introduction of other non-colour stimulus attributes had on the effectivity of chromatic masking stimuli. Previous studies of visual perceptual memory point to the involvement of separate systems in the retention of luminance and colour information (Shactler & Zaidi, 1993; Yoshizawa et al., 2011). Therefore, in an additional experiment we investigated the influence of adding luminance contrast to the chromatic masking stimuli. In the experiments described in this study so far, the mask, reference and test stimuli have all been equiluminant with the background. If the retention of chromatic and luminance contrast information does indeed occur within separate perceptual memory mechanisms then the prediction would be that the addition of luminance contrast to the masking stimulus should reduce its ability to interfere with the retention of colour information, i.e. the shifts in PSE should be reduced. To test this we repeated the delayed colour discrimination experiments using masking stimuli which varied in terms of their luminance contrast via manipulation of their luminance ratio (LR) (see methods). The data in figure 7 show how this affects measured PSEs and demonstrates that the greatest shift occurs when the mask, like the reference and test stimuli, is isoluminant (LR = 0.5) and contains no luminance contrast. When luminance contrast is added to the mask and LR increases or decreases from a value = 0.5, PSEs fall to levels similar to those obtained for the no mask condition. Thus, in line with the prediction, the addition of luminance contrast to masking stimuli renders them less effective in their ability to interfere with the retention of chromatic information. This is consistent with the idea that chromatic and luminance contrast are stored separately within short term perceptual memory.

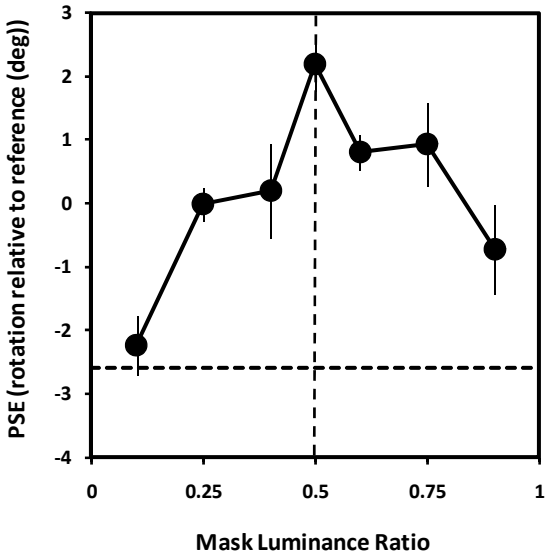

Figure 7. Memory masking as a function of luminance ratio. PSEs are plotted as a function of mask luminance ratio. The vertical dashed line represents the luminance ratio of the reference and test stimuli, as the luminance ratio tends towards zero the mask becomes a luminance contrast decrement stimulus. Towards a luminance ratio of 1 the mask becomes a luminance contrast increment. The data represent the average performance of 2 observers and the horizontal dashed line indicates baseline (no-mask) performance.

Discussion

In this study we have demonstrated using a memory masking paradigm the existence of selective, hue dependent, mask induced interference effects on stored representations of colour stimuli within short term visual perceptual memory. These findings suggest the existence of a short term perceptual memory system that can retain sensory information about stimulus colour which comprises an array of stores that retain chromatic information across limited bandwidths of colour space. These properties are consistent with previous studies which have demonstrated similar organisational principles for perceptual memory for other visual attributes such as spatial frequency and motion (Magnussen et al, 1991; Bennett & Cortese, 1996; Lalonde & Chaudhuri, 2002; McKeefry et al., 2007).

The existence of a perceptual or sensory memory system for the short term retention of colour information mirrors the extent to which colour has its own anatomically and physiologically distinctive processing pathway from the very earliest stages of visual processing. A number of previous studies have highlighted the fact that information about the colour of stimulus can be stored independently of other stimulus attributes, such as pattern and luminance (Nilsson & Nelson, 1981; Stefurak & Boynton, 1986; Sachtler & Zaidi, 1992; Magnussen et al., 1996, Cornelissen & Greenlee, 2000; Yoshizawa et al., 2011). Furthermore, humans are able to retain information about colour within short term memory with a high degree of accuracy over relatively long periods of time. However, colour memory is not perfect and when human subjects view a colour and then try to match it from memory after a period of time has elapsed, there are often slight, but measurable, differences between the original and memory matched colour in terms of hue, saturation and brightness (Collins, 1931; Burnham and Clark, 1954; Newhall et al., 1957; Bartleson, 1960; Siple and Springer, 1983; Jin & Shevell, 1996; Perez-

Carpinell et al., 1998; Nilsson & Nelson, 1981). More long-term memory representations of colour have also been shown to play an important role in the mechanisms that underpin colour constancy (Jin & Shevell, 1996; Ling & Hurlbert, 2008). In addition, there are the intriguing effects that have been demonstrated on low-level visual perception mediated by what have been termed 'memory colours' (Hansen et al. 2006) – a term which refers to the fact certain colours have a very close association with specific objects and are often integral to their identity.

Whilst the retention of colour information in short term perceptual memory undoubtedly provides us with a great deal of information about objects and surfaces within our environment, what do the experimental results reported here tell us about how this information is organised in short term perceptual memory? If we look at results from the spatial frequency domain, the bandwidths of tuning revealed by memory masking experiments have been found to be of the order of approximately +/- 1 octaves (Magnussen et al. 1991; Nemes et al 2011). This value is remarkably similar to estimates of bandwidths for spatial frequency channels that exist in low-level sensory visual processing, revealed by sensory masking and contrast adaptation studies (Campbell & Robson, 1968; Blakemore & Campbell, 1969; Blakemore et al., 1970; Blakemore & Nachmias, 1971; Georgeson & Harris, 1984). This correspondence has been taken as evidence to support the idea that there is close association between the sensory mechanisms that are involved in the low-level visual processing of spatial frequency and those that are involved in the storage of this information in perceptual or sensory memory (see: Pasternak & Greenlee, 2005 for a review). Following the same rationale, can the tuning revealed by the colour memory masking experiments in this study be linked with the sensory processing of colour in the visual system? We know that following photon capture

by the retinal photoreceptors, colour information is signalled by cone-opponent mechanisms (DeValois et al., 1966). These mechanisms rely upon linear combinations of L-, M- and S-cone inputs and predominate in the sub-cortical and early stages of cortical colour processing. Cone-opponent mechanisms exhibit responses to colour stimuli that vary sinusoidally across DKL colour space (Derrington et al., 1984; DeValois et al., 2000a). Figure 8a plots data recorded from such a cone-opponent (-L+M) neuron recorded from the monkey LGN (DeValois et al 2000b). Its response is plotted as a function of chromatic axis in DKL colour space and has been fitted by a Gaussian function which provides an estimate of bandwidth (σ). This gives a value of approximately 60°, typical of the bandwidth estimates for linear chromatic mechanisms found in sub-cortical and early V1 colour processing (D'Zmura & Knoblauch, 1998; DeValois et al., 2000a). This bandwidth, however, is considerably wider than those revealed in our memory masking experiments. Therefore, it seems unlikely that broadly tuned, linear cone-opponent mechanisms mediate these interference effects. Instead, an alternative basis for the for these effects might lie in the fact that rather than adhering to two cone-opponent or cardinal mechanisms, colour processing within the cerebral cortex instead relies upon multiple 'higher-order' chromatic mechanisms which are tuned to many different directions in colour space (Krauskopf et al., 1986; Webster & Mollon, 1991; DeValois et al., 1997; Zaidi & Halevy, 1993; Li & Lennie, 1997; Goda & Fuji, 2001: DeValois et al. 2000; Clifford et al, 2003; McGraw et al., 2004). These higher-order mechanisms appear to be the result of re-combinations of outputs from the cone-opponent mechanisms (see: Eskew, 2009 for a review). Currently, there is some debate as to whether they arise as the result of linear or non-linear interactions. Close to threshold, higher order mechanisms have been found to be largely linear with bandwidths of approximately 60°, similar to those exhibited by cone-opponent mechanisms (Sankeralli & Mullen, 1997; D'Zmura & Knoblauch, 1998; Giulianini & Eskew, 1998, Hansen & Gegenfurtner,

2006). On the other hand, at supra-threshold levels, there is evidence to suggest varying degrees of non-linearity in the formation of these higher order chromatic mechanisms, which leads to the generation of more narrowly tuned colour mechanisms with bandwidths of the order of 30-40° (Goda & Fujii, 2001; Clifford et al., 2003; McKeefry et al., 2004). These values are in closer accord with tuning characteristics revealed by the memory masking experiments in this study. Thus we might speculate that the chromatic information utilised by short term perceptual memory is derived from a stage in colour processing beyond that where the transformation from linear, broad-band, cone-opponent processing to non-linear, more narrow-band higher order chromatic processing has taken place. Narrowly tuned chromatic mechanisms are significant in colour processing in that they provide a potential link with specific hues – something that broad-band mechanisms do not offer. In order for more broadly tuned mechanisms to signal stimulus colour it would require another stage at which their outputs could be compared (Eskew, 2009). Outputs from narrowly tuned chromatic mechanisms, on the other hand, could directly signal stimulus hue. This link raises the possibility that colour information in short term perceptual memory is organised around perceptual colour categories. A similar suggestion has been made in the light of experimental findings which have demonstrated that the extent of degradation in the fidelity of remembered colours is less marked for more perceptually relevant or focal colours (Heider, 1972; Berlin & Kay, 1987; Nemes et al., 2010). Also consistent with this idea is the fact that hue naming functions, which were used in preliminary experiments in this study to define the reference stimuli, have bandwidths which are similar to those obtained from the colour memory masking experiments. In figure 8b, blue (p[blue]) and yellow p[yellow]) hue naming functions have been plotted as a function of chromatic axis. The values of σ obtained from the Gaussian fits reveal bandwidths of 41.8° for blue and 29.1° for yellow hue naming functions, comparable not only

to those values revealed by colour memory masking in this study, but also to those reported for non-linear, higher order chromatic mechanisms. Thus there is some circumstantial evidence to suggest that colour categories may form the basis for the storage of chromatic information in perceptual memory. However, there were discrepancies in terms of the bandwidth estimates between the memory masking and the hue naming data in the case of red and green stimuli. The hue naming functions (not shown) for red (p[red]) and green (p[green]) are much broader exhibiting plateaus across a range of colour space (see also: DeValois et al., 1997). This discrepancy may be a consequence of the fact that the hue naming method we employed restricted observer responses to only four basic colour categories (red, green, blue and yellow) to describe the stimuli. There is the possibility, therefore that these broader categories might consist of further sub-categories with narrower bandwidths, that may be more in keeping with the results revealed by memory masking. Certainly, further work will be required to establish more rigorously whether perceptual colour categories form the basis around which short term perceptual memory for colour is organised.

Experimental data from the primate visual system has not, as yet, provided us with an unequivocal answer as to where in the cortex the transformation or re-organisation from cone-opponent to perceptual colour coding might occur. At the single-unit level, studies have demonstrated that many cortical chromatic neurons exhibit colour tuning that is narrower than that found in the sub-cortical visual pathway (Thorell et al., 1984; Vautin & Dow, 1985; Lennie et al., 1990; DeValois et al., 2000a). The emergence of neurons that respond to specific perceptual colour categories appears to occur right from the level of V1 (Xiao et al., 2007) and they become more prominent in visual areas V2, V4 and posterior infero-temporal cortex (Zeki, 1980; Komatsu et al., 1992; Kiper et al., 1997; Xiao et al., 2003; Conway et al., 2007). In the

human brain, recent neuro-imaging studies have indicated that the transformation from cone-opponent to more perceptually based colour processing occurs at the level of visual areas V01 (ventral occipital) and V4 (Brouwer & Heeger, 2009). We suggest that these areas may constitute a possible locus for the neural activity that underpins short term perceptual colour memory. Certainly, area V4 has long been viewed (though not unanimously) as playing an important role in colour processing (Zeki, 1980; Lueck et al., 1989; McKeefry & Zeki, 1997; Wade et al., 2002; Brewer et al., 2004). Its involvement in colour perceptual memory, along with neighbouring areas in the ventral extra-striate cortex, would be consistent with perceptual memory being based upon neural activity based within a network of brain areas located beyond V1, but relatively early in the cortical processing stream (Fuster, 1997; Offen et al., 2009; Magnussen, 2009).

In summary, this study has examined the retention of chromatic information by short term visual perceptual memory. We have shown that the storage of chromatic information in this store is vulnerable to interference by the subsequent presentation of other chromatic stimuli. However, this interference is selective and is induced by stimuli that fall only within a relatively narrow range of colour space. These effects point to the involvement of narrowly tuned, non-linear, higher order chromatic mechanisms as the basis for the retention of colour information in short term perceptual memory.

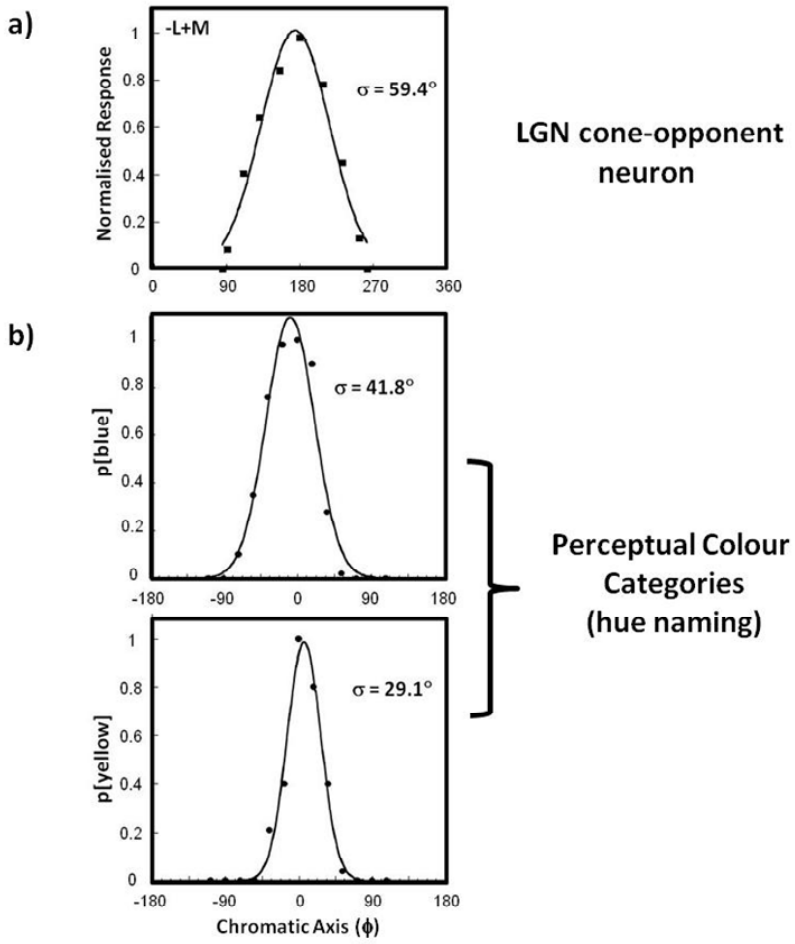

Figure 8. a) Responses of a cone-opponent (-L+M) LGN neuron plotted as a function of chromatic axis in DKL colour space. The data have been taken from DeValois et al. (2000b) and have been normalised and fitted with a Gaussian function, the bandwidth (i.e. the standard deviation) of which is specified by the parameter, σ.

b) Data taken from the hue naming experiment used in this study to define reference stimuli. The data points represent the proportion of times that colour stimuli were identified as, in these examples blue (p[blue]) and yellow (p[yellow]) as a function of chromatic axis (ϕ). Stimulus colour here is plotted in terms of relative rotation from the axis which defined the unique or exemplar hue. In the case of the blue colour naming data 0 refers to $\phi = 126^\circ$ in DKL colour space and $\phi = 286^\circ$ in the case of the yellow data. The functions represent the average data from 5 observers. As with the single-unit data shown in a) these behavioural data have been fitted with a Gaussian function in order to obtain bandwidth estimates (σ).

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