Running head: L/M-OPPONENCY AND VISUAL RECOGNITION

The L/M-Opponent Channel Provides a Distinct and Time-Dependent Contribution Towards Visual Recognition

Christopher J. Vincent, Fernand Gobet, Amanda Parker and Andrew M. Derrington

Abstract

The visual pathway has been successfully modelled as containing separate channels consisting of one achromatically opponent mechanism and two chromatically opponent mechanisms. However, little is known about how time affects the processing of chromatic information. Parametrically defined objects were generated. Reduced colour objects were interleaved with full-colour objects and measures of recognition performance (d-prime [*d'*]) were compared using the continuous serial recognition paradigm. Measures were taken at multiple delay intervals (1 s, 4 s, 7 s, and 10 s). When chromatic variations were removed, recognition performance was impaired, but at the 1 s and 10 s intervals only. When luminance variations were removed, no impairment resulted. When only L/M-opponent modulations were removed, a deficit in performance was produced only at the 1 s and 10 s intervals, similar to the removal of chromatic variation. When only S-opponent modulations were removed, no impairment was observed. The results suggest that the L/M-opponent pathway provides a specialized contribution to visual recognition, but that its effect is modulated by time. A three-stage process model is proposed to explain the data.

The L/M-Opponent Channel Provides a Distinct and Time-Dependent Contribution Towards Visual Recognition

Visual short-term memory (VSTM) relates to the ability to maintain information over a brief period of time. VSTM is limited in capacity (Gobet and Clarkson, 2004; Irwin 1992; Luck and Vogel 1997; Pashler 1988; Sperling 1960; Todd and Marois 2004) with undetermined representational characteristics (Lee and Chun 2001; Luck and Vogel 1997; Vogel et al 2001). Perceptual dimensions may be encoded within multiple parallel channels (e.g. psychophysical frameworks such as Magnussen and Greenlee 1997), or combined to form a single interrelated representation (e.g. hierarchical organised structural object descriptions; Marr and Nishihara 1978). Information stored in VSTM may use a subset of perceptual dimensions, some of which may be of weighted in terms of fidelity, novelty or content (Delvenne and Bruyer 2004; Delvenne and Dent 2008; Irwin 1992; Irwin and Andrews 1996; Lee and Chun 2001; Luck and Vogel 1997; Parker et al 1998; Vogel et al 2001; Wheeler and Treisman 2002).

We wanted to examine whether constraints placed on a single dimension (colour) modulated VSTM performance. Understanding VSTM and its role in recognition ability is important as it has the potential to aid normal and deficient behaviour. In this study, the contribution of colour to human visual recognition performance was examined to ascertain the effect of time on removing variation from object stimuli along one or two dimensions of the 3D colour space.

Chromatic variations provide the visual system with the means to gain invariance and specificity, colour having been shown to provide benefit in visual segmentation, recognition, identification and classification (Davidoff and Oostergaard 1988; Gegenfurtner and Rieger 2000; Gegenfurtner et al 1998; Kingdom 2003;

Oostergaard and Davidoff 1985). Conversely, studies have shown that luminance cues support the recognition of faces, objects and scenes (Oliva and Schyns 1997; Parker et al 1998; Parker et al 1992; Schyns and Oliva 1994, 1997, 1999; Sergent 1986). The question remains as to whether the reduced temporal and spatial sensitivities of chromatic opponency (particularly S-cone-opponency) result in chromatic cues being diagnostic or of limited use (Anglin and Levie 1985; Biederman and Ju 1988; Tanaka and Presnell 1999). What is the comparative contribution of chromatic, L/M-opponent, S-opponent and achromatic modulations to object recognition?

The visual pathway has been successfully modelled as containing separate channels consisting of one achromatically opponent mechanism and two chromatically opponent mechanisms (Buchsbaum and Gottschalk 1983). Empirical evidence shows that contrast sensitivity functions for stimuli containing achromatic, L/M-opponent and S-opponent modulations take differing forms, reflecting differences in the properties of the mechanisms that convey each class of signal (Mullen 1985). Adapting stimuli that isolate one of the opponent mechanisms do not alter visual threshold measurements taken along the orthogonal opponent direction (Bradley et al 1988; Krauskopf and Gegenfurtner 1992; Krauskopf et al 1982). Differences in performance have been observed in shape discrimination tasks, measuring the radial modulation threshold for discrimination between circular and non-circular stimuli matched in multiples of stimulus detection threshold. The S-opponent system was found to perform worst, followed by the L/M-opponent system and the achromatic system (Mullen and Beaudot 2002).

Imaging studies using functional magnetic resonance imaging (fMRI) have shown how extremely sensitive the visual system is to chromatic modulations of low spatial and temporal frequencies. Stimuli expressed in terms of vector length in cone contrast space require differing levels of modulation to produce similar V1 BOLD response (9:60 ratio for L/M-opponent versus luminance modulation; Liu and Wandell 2005; Parkes et al 2009).

In spite of clear progress in understanding the mechanisms underpinning chromaticy, we do not know whether these mechanisms interact with time (beyond the spatial temporal properties of the early visual pathway; Kelly 1974). Does colour help recognise an object as previously seen to the same extent after 1 s, 5 s or 10 s? This gap in knowledge is surprising, as such an interaction would affect what kinds of objects are differentially recognized in the short term and long term, which would obviously have evolutionary implications. In addition, understanding such an interaction would shed light on the role of colour in VSTM and could have practical implications.

In this study, we examined how time affects the relative contribution of the L/M-opponent and S-opponent modulations to visual recognition. We were interested in the degree to which time modulates the effect of signals conveyed by each of the separate opponent mechanisms on visual recognition memory. Flower-like objects were used as stimuli. The use of naturalistic stimuli was critical, as many laboratory-based studies have been criticized for their lack of ecological validity. The stimuli were constrained such that they were trial-unique and contained a high level of feature ambiguity.

With these stimuli, we removed the signals that were conveyed by one of the opponent or luminance pathways. This allowed the contribution of chromatic and achromatic variations to recognition memory to be assessed. By removing L/M-opponent, S-opponent or achromatic variations from stimuli, we could examine their effect upon recognition performance and therefore compare the relative contribution of signals conveyed by each of the mechanisms. The use of the continuous serial recognition paradigm (Shepard and Teghtsoonian 1961) allowed study and test objects to be presented over multiple delay intervals. By manipulating the delay intervals, we could assess the extent to which effects of chromatic or achromatic subtraction were persistent over time.

Method

Overview

Participants were tested on two types of task. The first task measured visual thresholds along the cardinal directions of Derrington, Krauskopf and Lennie (DKL) colour space (Derrington et al 1984). The data were saved in order to construct the stimuli used in the second task and thus equate stimuli in terms of visual threshold. The second task required participants to make novel or familiar judgments when presented with interleaved study and test object stimuli, produced using a restricted or unrestricted colour space. Four groups performed the serial recognition task, each observing full-colour objects and objects that either lacked all chromatic variations (Group 1), luminance variations (Group 2), L/M-opponent variations (Group 3), or S-opponent variations (Group 4). Objects that lacked variations in a specific part of colour space (e.g., L/M-opponent variations) contained variations along the two other parts of colour space (e.g., S-opponent and luminance variations) (Figure 1). Different exemplars of the objects were used for the full-colour stimuli and manipulated stimuli. We chose a between-participant design, where participants were tested on full-colour objects and a single class of manipulated objects, after a pilot study indicated that a within-participant design, where each participant received the four classes of stimuli, encouraged participants to use categorical methods to remember objects.

Participants

Forty-seven participants from the University of Nottingham campus volunteered. Each participant was assigned to one of the four experimental groups detailed in Figure 1, such that there were 10 or more participants in each group. There were also similar numbers of male and female participants in each of the groups. All participants reported that they had normal or corrected to normal vision and normal colour vision. We used the output from the threshold task to screen for any colour deficient observers (e.g., anomalous trichromats).

Apparatus

The tasks ran on a dual processor G4 Macintosh computer (Macintosh UK). Participants provided responses via a two-button mouse (Kensington US). Feedback was provided using the computer's in-built speaker. The experimental programs were produced using MATLAB 5.2 (Mathworks UK), along with the additional PsychToolbox routines (Brainard 1997). Experimental timing was derived from the system clock. Stimuli appeared on a Mitsubishi Diamond Pro monitor (Mitsubishi UK) driven by a Radius Golden Gate video card. Screen resolution was set at 640 by 480 pixels. A refresh rate of 60 Hz was used. Measurements of screen luminance and chromaticity were obtained using a PR-650 spectral radiometer (PhotoResearch US). The maximum achievable luminance output of the monitor was 83.27 cd/m^2.

The video card used was a Radius Golden Gate video card. The card provided 1024 levels of output per gun (10 bit). The linearization method for the monitor output was reliant on a gamma curve fit to within a root mean square (RMS) error of 0.9985, as reported by the PsychToolbox linearization functions. Similar functions were used to map from device specific co-ordinates to DKL co-ordinates (Brainard 1997). The Commission Internationale d'Eclairage (CIE) co-ordinates of the maximum monitor gun output were (xyY); Red: (0.61, 0.35, 18.23); Green (0.31, 0.60, 55.40); and Blue (0.15, 0.07, 10.77).

Procedure

Task 1: Visual Threshold Task.

The threshold task lasted approximately 10 minutes. Threshold sessions used a self-paced, two-choice procedure, where a single stimulus was presented at a time. Participants were presented with a three-ellipse object (study object) for 2 s. Then, for a short delay (1 s), there was a uniform grey background (xyY = 0.28, 0.29, 41.63) A fixation cross was located at the centre of the screen (co-ordinates: 310 and 245 pixels).

The fixation cross was then removed and an object was presented (test object), identical in every respect to the study object other than the addition of a fourth element of variable contrast. Participants reported whether the two objects were similar or dissimilar. The constituent ellipses were approximately 65 pixels by 12 pixels in size and viewing distance was set to 57 cm. Participants' responses made it possible to infer the visibility of the variable contrast element within the test object. If the element was supra-threshold, then participants would report the objects as dissimilar; if the element was sub-threshold, then they would report the objects as similar.

The three-element objects consisted of ellipses oriented at an angle of 0°, 90°, 180°, or 270°. The vacant position was chosen using a pseudo-random algorithm. Test objects contained ellipses positioned at 0°, 90°, 180° and 270° angle. Three out of the four ellipses were set to the same size, orientation and contrast as the preceding study object. The fourth ellipse was placed in the position that was vacant in the study object. The contrast of this ellipse was varied over time, according to a staircase procedure. When participants reported that the study and test objects were similar, the contrast of the manipulated ellipse was increased. This continued until participants reported that the study and test objects were dissimilar on more than 15% of trials. The direction of contrast change was then reversed, and the step size of the change was halved. This procedure was repeated until the contrast change reached the minimum level allowed by the device, at which point the threshold was recorded and the axis of DKL colour space along which the threshold was being determined was changed.

Thresholds were consecutively defined upon the line determined by the grey background and the endpoint of each of the DKL axes. As the objects used in the serial recognition task contained ellipses specified by a range of chromatic and/or achromatic contrasts, the objective of the threshold task was to produce objects that were theoretically equivalent in the way they excited the fundamental parts of the visual system. For a more thorough treatment, see Cole et al (1993) and Mullen (1985). The method of single stimuli used here may have allowed criterion changes that were not monitored.

Task 2: Serial Recognition Task.

The serial recognition task consisted of a modified version of the paradigm developed by Shepard and Teghtsoonian (1961). It consisted of two sessions, each session containing 406 trials and lasting for 20 minutes. The sessions measured participant performance in discriminating trial-unique flower-like objects. The effects of two variables on discrimination performance were examined:

1. The effect of increasing the delay interval between study and test objects.
2. The effect of restricting the various types of visual modulations used to display the object.

Based on the measurements taken in the threshold task, we artificially generated parametrically defined objects that resembled flowers (Figure 1). These objects were designed such that they contained a high level of feature ambiguity and were difficult to recognize using structural cues alone. Objects were produced by overlaying between 3 and 45 ellipses of specified size, aspect ratio, orientation, position, DKL elevation, azimuth and magnitude. Ellipses were solid: when they overlapped, no colour-mixing algorithm applied. Ellipses were chosen because they resemble the type of stimuli that are effective in eliciting a (cellular) response in primary visual cortex (Hubel and Wiesel 1962).

Each of the defining parameters (other than the DKL vector) was constrained and chosen from a probabilistic normal distribution so that the objects were trial-unique. For each participant, DKL vectors were defined in terms of multiples of the threshold values obtained from the threshold task. All vectors were set so that their magnitude was between two and four times the interpolated participant threshold value. This range was chosen based on a series of pilot studies designed to find stimuli that were sufficiently distinctive to induce steady state recognition whilst avoiding ceiling effects. Contrast levels were also constrained to avoid exceeding the gamut of the monitor. All DKL vectors were drawn between the mid-point of the space in the direction of the negative end of the luminance axis (e.g. in the bottom half of the sphere). The effect of negative deviations was expected to mirror the effect of positive deviations (Burkhardt et al 1984). These values may not reflect the distribution of contrast in the natural world and future work could examine how spectra from natural scenes could be used to define the vectors.

All stimuli (study and test objects) remained on screen for 2 s, with an intervening uniform grey background replacing the object for 1 s between trials. Test objects were presented after the study objects, using one of four delay intervals. Test objects reappeared either immediately after the study object, or after 1, 2 or 3 intervening objects. The delay interval between study and test items therefore lasted for 1, 4, 7, or 10 s. Where possible, intervening objects were study or test objects for the following or previous objects. Where this was not possible (in less than 2% of presentations), novel objects were presented that were never tested (i.e., at the end of the task). In all cases (on every stimulus presentation), the participants' task was to indicate, by pushing one of two buttons, whether the stimulus was novel or familiar (new or old). Participants were not instructed about the underlying design of the task (e.g., that objects were repeated after 0, 1, 2 or 3 intervening objects) (Figure 2).

The two sessions contained equal numbers of study and test items. Equal numbers of study and test items were also assigned to each of the delay intervals. Equal numbers of colour object and visually restricted objects were tested at each of the delay intervals.

Stimuli were restricted in their visual properties so they lacked:

1. Colour: Greyscale stimuli that only contained variations in luminance.

2. Luminance: Isoluminant stimuli that only contained variations in chromaticity. These stimuli were obtained by removing all variations along the luminance axis in DKL space.

3. L/M-opponent modulations: Stimuli that contained S-opponent and luminance variations.

4. S-opponent modulations: Stimuli that contained L/M-opponent and luminance variations.

Each group of participants were tested on a set of objects containing, for one half, stimuli with variations in colour and luminance (full-colour stimuli) and, for the other half, stimuli constrained by one of the four restrictions described above. This allowed the within-group comparison of full-colour objects and objects produced using a restricted colour space. There were therefore four separate groups of participants performing similar versions of the task.

Data Analysis

Thresholds were recorded in terms of a DKL contrast value using the routines included in the PsychToolbox. Participant responses for the serial recognition task were categorized into four types of response (hits, misses, correct rejections, and false alarms). Participant performance in each of these categories was then used to calculate a measure of recognition performance (*d'*) based upon signal detection theory. This value was used as an indicator of performance over the experimental manipulations. Participants' data were discarded from the serial recognition sessions if the average *d'* score in the first delay interval was below 2, or if average *d'* score for full-colour objects was negative. For the first delay interval, the stringent criteria (*d'* < 2) was chosen as, normally, participants performed near perfectly, so a relatively low *d'* score suggested a lack of engagement with the task. Seven participants were discarded using these criteria.

Statistical analyses were carried out in SPSS. Rather than carrying out an omnibus analysis of variance (ANOVA), we performed separate repeated-measures ANOVA for each of the four groups. We chose to analyze the data in this way to maintain an independent comparison between full-colour, un-manipulated objects and each class of visually restricted object.

Results

Visual Threshold Task

The highest threshold value (or lowest contrast sensitivity) was produced for blue objects (DKL ΔR_S[1] = 0.1275, SEM = 0.0073) followed by yellow objects (DKL ΔR_S = 0.0988, SEM = 0.0039), black objects (DKL ΔR_{LUM} = 0.0503, SEM = 0.0026), green objects (DKL $\Delta R_{L\text{-}M}$ = 0.0169, SEM = 0.00088) and red objects (DKL $\Delta R_{L\text{-}M}$ = 0.0130, SEM = 0.00096). A Greenhouse-Geisser corrected ANOVA was run on the data from all groups to assess for significant differences in threshold level. A significant main effect of threshold colour was observed $F(1.463, 65.848) = 223.91$, $p < .001$. Bonferroni-corrected pairwise comparisons revealed significant differences at the .001 level between all of the threshold types.

Serial Recognition Task

For the serial recognition paradigm, overall memory performance was found to be reliable. Participants provided a correct response to the colour objects on 78% of trials (SEM = 1.4%). Performance for full-colour objects averaged over all delay intervals did not vary greatly over Groups 1-3 (Group 1: *d'* = 1.98; Group 2: *d'* = 1.84; and Group 3: *d'* = 1.80). For Group 4, overall performance was slightly higher (*d'* = 2.12). When results were averaged over the groups and over all delays, little difference was observed between correctly identifying previously seen objects (Hits = 77.74%) and correctly rejecting new objects as being unfamiliar (Correct rejections = 78.18%).

The Removal of Chromatic Variations, but Not Luminance, Impairs Recognition Performance at Short and Long Delay Intervals

Results from Group 1 (full-colour objects versus greyscale objects) were designed to establish whether the removal of stimulus chromaticity had a negative effect on

---

[1] ΔR represents mechanism pooled cone contrast (Brainard 1996)

recognition ability and whether this was present across all delay intervals or specific to some of them. When recognition performance was compared for full-colour objects and objects lacking chromatic variations, a drop in discrimination performance was observed (Figure 3, left hand-side). The ANOVA showed a significant main effect of chromatic removal $F(1,9) = 9.148$, $p < .05$, $p_{rep} = .94$, $\eta^2 = .50$. Participants produced significantly higher scores with coloured stimuli, *d'* = 2.08, *SEM* = 0.260, than with greyscale stimuli, *d'* = 1.655, *SEM* = 0.336.

For both colour and greyscale objects, recognition performance decreased over successive delays. This effect was highly significant: $F(3,27) = 26.4$, $p <.001$, $p_{rep} = .99$, $\eta^2 = .75$. A significant interaction was found between the stimulus manipulation and the delay interval $F(3,27) = 3.923$, $p < .05$, $p_{rep} = .93$, $\eta^2 = .30$. The effect of colour removal was statistically significant at the 1 s interval, $F(1,9) = 18.331$, $p < .005$, $p_{rep} = .98$, $\eta^2 = .67$, and at the 10 s interval, $F(1,9) = 5.12$, $p = .05$, $p_{rep} = .88$, $\eta^2 = .36$. It was not statistically significant at the 3 s interval, $F(1,9) = 0.363$, *ns*, nor at the 7 s interval, $F(1,9) = 0.123$, *ns*. Figure 5 shows the ratio of *d*' for the full-colour stimuli to the *d'* for the greyscale stimuli, as a function of delay interval. Cleary, the curve follows a quadratic function ($r^2 = .97$).

When luminance (greyscale) variations were removed from stimuli (Group 2; see Figure 3, right-hand side), no drop in discrimination performance was observed. Removal of luminance modulations had no effect on participant discrimination performance, colour *d'* = 1.800, *SEM* = 0.217; isoluminant *d'* = 1.698, *SEM* = 0.1698, $F(1,9) = 1.581$, *ns*. As with full-colour objects, increasing delay interval impaired recognition performance, $F(3,27) = 75.364$, $p < .001$, $p_{rep} = .99$, $\eta^2 = .893$, but there was no interaction between colour manipulation and delay interval $F(3,27) = 1.227$, *ns*.

Removal of L/M-Opponent Variations, but not S-Opponent Variations, Impairs Ability at the Shortest and Longest Intervals

Results from Group 3 (full-colour objects versus objects lacking L/M-opponent modulations) were intended to test the hypothesis that L/M-modulations provided a specific contribution to recognition performance. When L/M-opponent variation was removed from the stimuli, participants displayed a deficit in their capacity to recognize subsequently repeated stimuli when compared to performance with full-colour objects (see Figure 4, left-hand side). A significant main effect of the removal of L/M-opponent variation was observed, $F(1,9) = 5.119, p < .05, p_{rep} = .88, \eta^2 = .36$. Participants performed significantly better with full-colour stimuli, *d*' = 1.783, *SEM* = 0.160, than with stimuli lacking L/M-opponent variations, *d*' = 1.568, *SEM* = 0.159. As with the other classes of objects, recognition performance significantly decreased as the delay interval increased, $F(3,27) = 49.4, p < .001, p_{rep} = .99, \eta^2 = .85$. A significant interaction between stimulus type and delay interval was also found in the full-colour vs. stimuli lacking L/M-opponent variations group, $F(3,27) = 4.225, p < .05$ $p_{rep} = .94, \eta^2 = .32$. The main effect of the removal of L/M-opponent variations was statistically significant at the 1 s interval, $F(1,9) = 9.257, p < .05, p_{rep} = .94, \eta^2 = .51$, and at the 10 s interval $F(1,9) = 5.806, p < .05, p_{rep} = .89, \eta^2 = .39$. However, there was no such effect at the 3 s interval $F(1,9) = .005$, *ns*, nor at the 7 s interval, $F(1,9) = .046$, *ns.* Figure 5 shows the ratio of *d'* for the conditions containing full-colour stimuli and stimuli lacking L/M-opponent modulation, as a function of delay. Just like with Group 1, the curve is well fitted by a quadratic function ($r^2 = .97$).

The removal of S-opponent modulations (Group 4, see Figure 4, right-hand side) had little or no effect on recognition performance. In fact, in three out of four of the delay conditions, the removal of S-opponent modulations increased the mean recognition score. Therefore, a main effect of stimulus colour removal was not found for the group comparing full-colour stimuli (*d*' = 2.075, *SEM* = 0.242) with stimuli lacking S-opponent modulations (*d*' = 2.180, *SEM* = 0.208), *F*(1,9) = 0.528, *ns*. This contrasted with effects of removing L/M-opponent modulations. As with all of the other conditions relating to chromatic restriction, participants showed a significant drop in recognition performance over delay interval, *F*(3,27) = 59.0, $p < .001$, $p_{rep} = .99$, $\eta^2 = .87$. There was no interaction between colour manipulation and delay interval, *F*(3,27) = 1.5, *ns*.

In order to further examine effects of chromatic removal, analysis was conducted that sought to quantify between-participant effects. When effects of chromatic manipulation were examined between groups (specifically Groups 3 and 4, where effects of chromatic removal had and had not been observed) a significant effect was observed between performance on objects lacking L/M-opponent modulations (*d*' = 1.568, *SEM* = 0.159) compared with those lacking S-opponent modulations (*d*' = 2.180, *SEM* = 0.208), F(1,18) = 5.484, $p < .05$, $p_{rep} = .91$, $\eta^2 = .23$. Thus, participants performed worse with stimuli lacking L/M-opponent modulations than with stimuli lacking S-opponent modulations.

In Group 4, there was a trend for performance in the full-colour condition at 3, 7 and 10 s delays to be better than in Group 3. There is a possibility that performance with the full-colour objects could have been facilitated as a result of comparatively better performance with the restricted objects. A between-group design testing each class of objects independently would have mitigated against this possibility.

Discussion

The most arresting result of our study was that, while the removal of colour and L/M-opponent modulations affected recognition, the effect was present only with the 1 s and 10 s intervals, with a larger effect at 1 s. When plotting the *d'* ratios of the full-colour condition to the manipulated condition as a function of delay interval, a quadratic relation was apparent (Figure 5). A similar relation was apparent with Groups 2 and 4, with the qualification that the *d'* ratios were close to 1, indicating lack of superiority of the full-colour condition. Why is this effect not present at medium-time intervals, and why is it present with the removal of L/M-opponent modulations but not S-opponent modulations?

Effects of Chromatic Subtraction Vary Over Delay Interval

We suggest that a three-stage process is involved in the effects observed in this study. At very short delay intervals (1 s), the participants hold the visual characteristics of the objects in iconic memory (Sperling 1960; Phillips 1974). Numerous studies have shown that iconic memory can store a large amount of information until about 1 s, with rapid decay.

At the 3 s and 7 s delay intervals, the difference in performance for full-colour and chromatically restricted objects is attenuated. We suggest that small amounts of information are held in VSTM, in a ready available state, probably supplemented by verbal descriptions held in auditory short-term memory (ASTM; Mackworth, 1964). Our chromatic manipulations appear to have no differential effect at these delay intervals, implying that the recognition ability is not modulated by the VSTM encoding chromaticity. This converges with accounts of the limited capacity of VSTM noted in the introduction.

At the 10 s delay interval, the trend observed at the 1 s delay interval returns. At this point, most of the visual information held in VSTM and the verbal descriptions held in ASTM have been replaced by information about the following stimuli, with the consequence that participants must rely on long-term memory. It is proposed that stimuli traces have been consolidated to a point where the chromatic variations are of use. Associations of this nature relate to chunking mechanisms (Gobet et al 2001), which have been simulated and validated by computational models such as CHREST (CHunk Hierarchy and REtrieval STructures; Waters and Gobet 2008). CHREST assumes that encoding a chunk into LTM takes between 8 s and 10 s, and the differential effects observed in our results supports this assumption.

In a study investigating the contribution of colour to recognition memory for natural scenes, Wichmann et al (2002) show that colour provides superior recognition ability for images of natural scenes and exclude the possibility that this is a result of saliency or attentional factors. They also show that the benefit depends on the colour congruency of the presented image with participants' experience. They suggest two memory components, an achromatic structural description system alongside a surface-based episodic system storing colour information that accords with knowledge. In our study, the L/M-opponent advantage was present at short (sensory) and long delays (episodic), which concurs with this account.

The Contribution of L/M-Opponent Modulations Versus S-Opponent Modulations in Object Recognition

At short delay intervals, the removal of L/M-opponent modulations clearly impaired performance. When we removed S-opponent modulations from the stimuli, no such effect was observed. Differential performance in shape discrimination based upon selective use of the L/M-opponent or S-opponent mechanisms has been observed by other studies (Mullen and Beaudot 2002), showing the L/M-opponent system to be superior to the S-opponent system. This could be a result of the reduced spatial resolution of the S-opponent mechanism. The density of the three cone classes varies with eccentricity and is higher for the long-wavelength-sensitive (L) and medium-wavelength sensitive (M) cones than for the cones sensitive to short-wavelength (S) light. This limits the spatial frequency that the S cone mosaic can represent (Wandell 1993).

The S-opponent pathway is also thought to be sluggish compared to the L/M-opponent pathway (Cottaris and De Valois 1998). This difference is small (20-30 ms) when estimated from visually triggered reaction time (RT) for briefly presented visual stimuli confined to chromatic channels and presented at equivalent threshold levels (Smithson and Mollon 2004). We did not find any differences in RT for any of the classes of object tested, and suggest that a combination of the static nature of stimulus presentation combined with the period between study and test reduces the likelihood of finding differences in RTs.

We suggest that the L/M-opponent pathway has differing functional characteristics to the S-opponent or achromatic mechanisms. The L/M-opponent and S-opponent systems evolved at separate time periods, and some authors suggest that specific evolutionary pressures shaped the phylogenetically distinct L/M-opponent ability. These include the need to detect fruit from foliage (Barlow and Mollon 1982) or ripe from unripe leaves (Lucas et al 2003). In their study on the stability of colour-opponent signals under changes of illuminant in natural scenes, Lovell and colleagues discuss a number of functional roles of the opponent colour systems. These include gaining information about the material (reflectance) properties of objects by removing “noise” from shadows or changes in illumination. The authors suggest that the L/M-opponent system is more effective in this respect during daylight viewing conditions, being robust to the blue tint present in shadows and sensitivity to discriminating fruits from inedible leaves (Lovell et al 2005). In our study, we found a recognition advantage for the L/M-opponent system at very short delay intervals, which corresponds to the sensory contribution aligned with this account.

In conclusion, we propose that L/M-opponency forms the basis of a functionally distinct representation, which could sub-serve an increased ability to recognize and discriminate naturalistic objects and object properties. The effect could be underpinned by differential modulation of the sensory buffer (iconic memory) caused by the presence (or lack of) L/M-opponent modulations. This is worthy of further investigation given the fact that the effect of subtracting L/M-opponent variations was most pronounced at the shortest delay interval.

Figure Captions

Figure 1. Example of the stimuli used in each of the experimental groups. Top row, Column 1 = full-colour (baseline). Top row, Column 2 = greyscale / minus chromaticity (Group 1). Middle row, Column 1 = minus L/M-opponent modulations (Group 3). Middle row, Column 2 = minus S-opponent modulations (Group 4). Bottom row, minus luminance (Group 2).

Figure 2. Experimental sessions: 1) Threshold sessions, determining discrimination thresholds for the cardinal axes of DKL space. 2) Serial recognition task. Green boxes are study trials (novel objects) red boxes are test trials (familiar objects). Participants provide novel or familiar response on every stimulus presentation.

Figure 3. Participant *d'* scores for Groups 1 and 2. Hatched bars = performance on full-colour objects. Grey bars = performance on objects lacking chromatic modulations. White bars = performance on objects lacking achromatic modulations. Standard error bars refer to ± 1 *SEM*.

Figure 4. Participant *d'* scores for Groups 3 and 4. Hatched bars = performance on full-colour objects. Grey bars = performance on objects lacking L/M-opponent modulations. White bars = performance on objects lacking S-opponent modulations. Standard error bars refer to ± 1 *SEM* .

Figure 5. Ratios in *d'* scores for full-colour and manipulated objects across all groups.

Figure 1 (TOP)

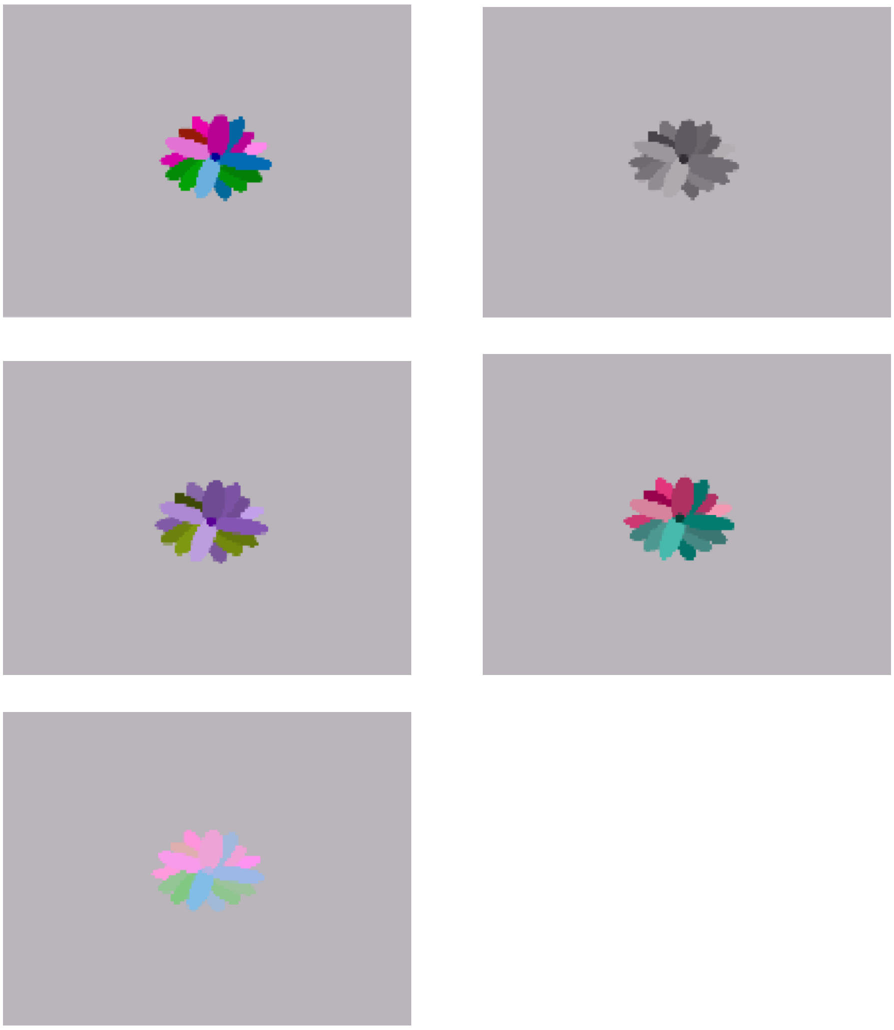


Figure 2 (TOP)

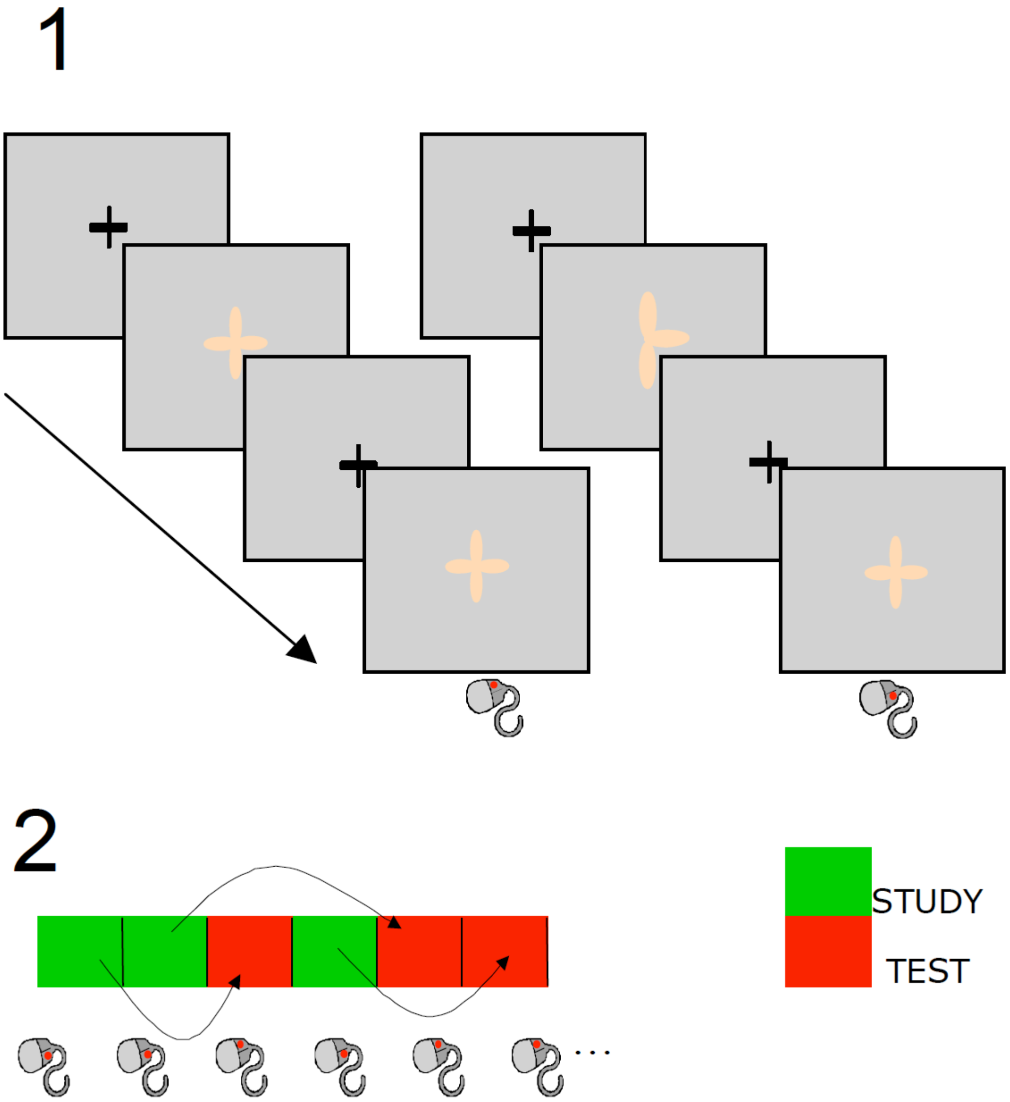


Figure 3 (TOP)

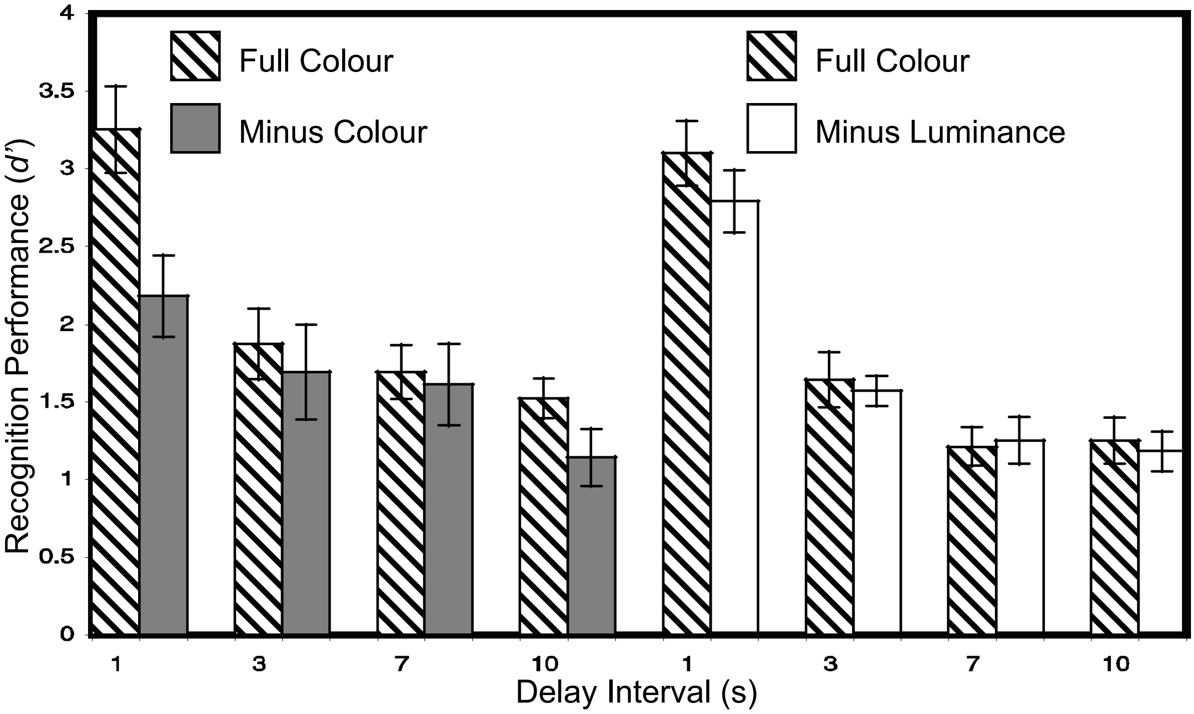

Full Colour
Minus Colour
Full Colour
Minus Luminance
Recognition Performance (d′)
4
3.5
3
2.5
2
1.5
1
0.5
0
1
3
7
10
1
3
7
10
Delay Interval (s)

Figure 4 (TOP)

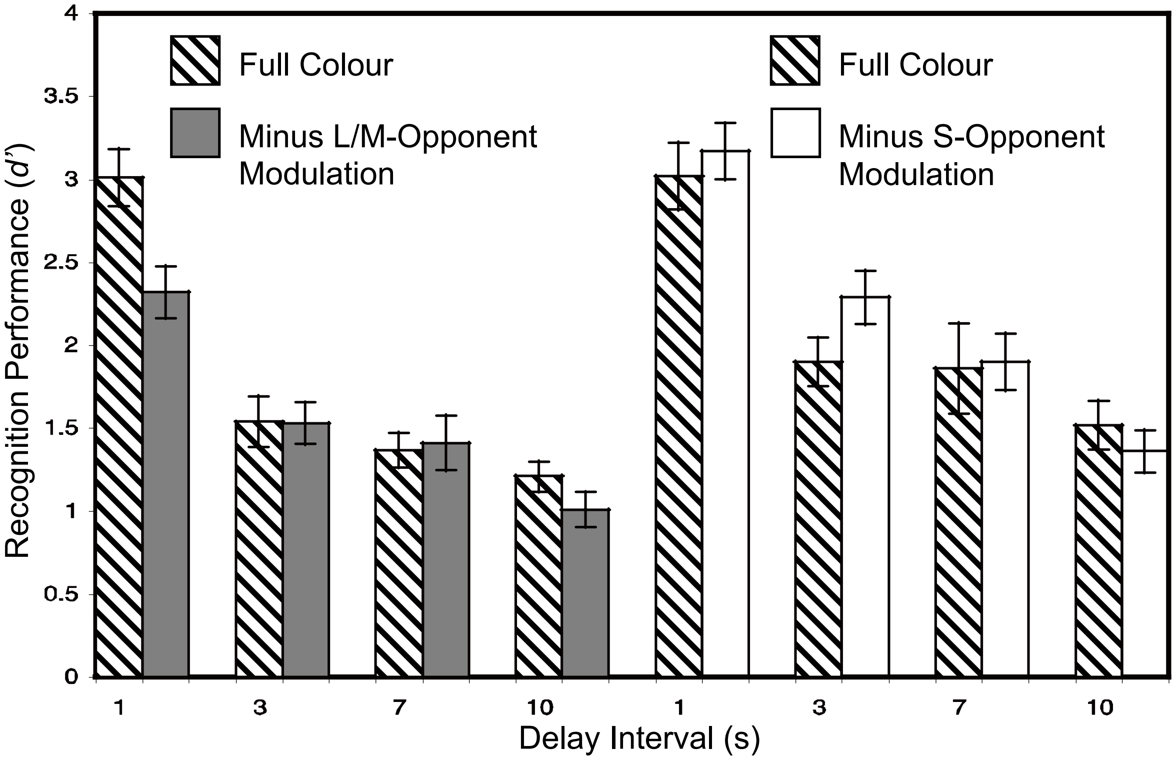
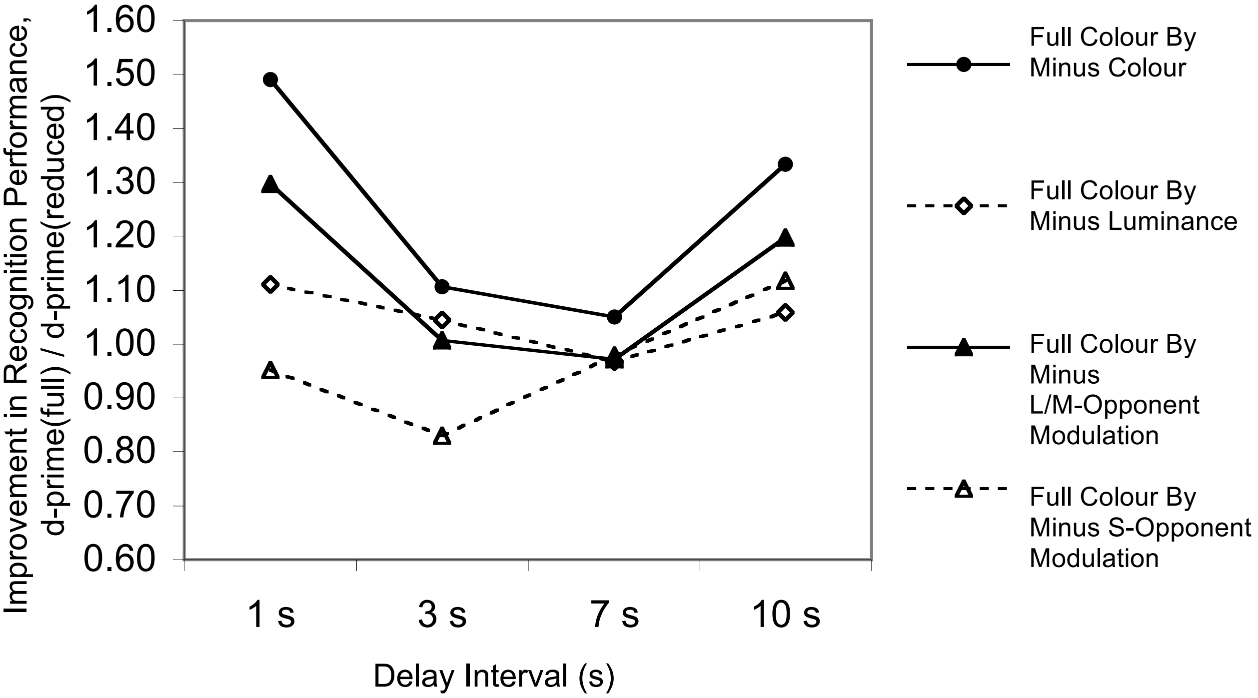

Full Colour
Minus L/M-Opponent Modulation
Full Colour
Minus S-Opponent Modulation
Recognition Performance (d')
0
0.5
1
1.5
2
2.5
3
3.5
4
1
3
7
10
1
3
7
10
Delay Interval (s)

Figure 5 (TOP)


Improvement in Recognition Performance, d-prime(full) / d-prime(reduced)
1.60
1.50
1.40
1.30
1.20
1.10
1.00
0.90
0.80
0.70
0.60
1 s
3 s
7 s
10 s
Delay Interval (s)
Full Colour By Minus Colour
Full Colour By Minus Luminance
Full Colour By Minus L/M-Opponent Modulation
Full Colour By Minus S-Opponent Modulation

Anglin G J, Levie W H, 1985 "The role of visual richness in picture recognition memory" *Perceptual and Motor Skills* **61** 1303-1306

Barlow H B, Mollon J D, 1982 *The Senses* (Cambridge, MA: Cambridge University Press)

Biederman I, Ju G, 1988 "Surface versus edge-based determinants of visual recognition" *Cognitive Psychology* **20** 38-64

Bradley A, Switkes E, De Valois K, 1988 "Orientation and spatial frequency selectivity of adaptation to color and luminance gratings" *Vision Res* **28** 841-56

Brainard D H, 1996 “Cone contrast and opponent modulation color spaces”, in *Human Color Vision, 2nd edition* Eds P K Kaiser and R M Boynton, (Washington, DC: Optical Society of America)

Brainard D H, 1997 "The Psychophysics Toolbox" *Spat Vis* **10** 433-6

Buchsbaum G, Gottschalk A, 1983 "Trichromacy, opponent colours coding and optimum colour information transmission in the retina" *Proceedings of the Royal Society London B* **220** 89-113

Burkhardt D A, Gottesman J, Kersten D, Legge G E, 1984 "Symmetry and constancy in the perception of negative and positive luminance contrast" *J Opt Soc Am A* **1** 309-16

Cole G R, Hine T, McIlhagga W H, 1993 "Detection mechanisms in L-, M-, and S-cone contrast space" *J Opt Soc Am A* **10** 38-51

Cottaris N P, De Valois R L, 1998 "Temporal dynamics of chromatic tuning in macaque primary visual cortex" *Nature* **395** 896-900

Davidoff J B, Oostergaard A L, 1988 "The role of colour in categorical judgements" *Quarterly Journal of Experimental Psychology: Human Experimental Psychology* **40** 533-544

Delvenne J F, Bruyer R, 2004 "Does Visual Short-Term Memory store bound features?" *Visual Cognition* **11** 1-27

Delvenne J F, Dent K, 2008 "Distinctive shapes benefit short-term memory for color associations, but not for color." *Perception & Psychophysics* **70** 1024-1031

Derrington A M, Krauskopf J, Lennie P, 1984 "Chromatic mechanisms in lateral geniculate nucleus of macaque" *J Physiol* **357** 241-65

Gegenfurtner K R, Rieger J, 2000 "Sensory and cognitive contributions of color to the recognition of natural scenes" *Curr Biol* **10** 805-8

Gegenfurtner K R, Wichmann F A, Sharpe L T, 1998 "The contribution of color to visual memory in X-chromosome-linked dichromats" *Vision Res* **38** 1041-5

Gobet F, Clarkson G, 2004 "Chunks in expert memory: Evidence for the magical number four… or is it two?" *Memory* **12** 732-747

Gobet F, Lane P C, Croker S, Cheng P C, Jones G, Oliver I, Pine J M, 2001 "Chunking mechanisms in human learning" *TRENDS in Cognitive Sciences* **5** 236-243

Hubel D H, Wiesel T N, 1962 "Receptive fields, binocular interaction and functional architecture in the cat's visual cortex" *J Physiol* **160** 106-54

Irwin D E, 1992 "Memory for position and identity across eye movements" *J Exp Psychol Learn Mem Cogn* **18** 307-317

Irwin D E, Andrews R, 1996 "Integration and accumulation of information across saccadic eye movements", in *Attention and performance XVI: Information integration in perception and communication* Eds T Inui and J L McClelland (Cambridge, MA: Cambridge, MA)

Kelly D H, 1974 "Spatio-temporal frequency characteristics of color-vision mechanisms," *J Opt Soc Am* **64** 983-990

Kingdom F A, 2003 "Color brings relief to human vision" *Nat Neurosci* **6** 641-4

Kleinschmidt A, Lee B B, Requardt M, Frahm J, 1996 "Functional mapping of color processing by magnetic resonance imaging of responses to selective P- and M-pathway stimulation" *Exp Brain Res* **110** 279-88

Krauskopf J, Gegenfurtner K, 1992 "Color discrimination and adaptation" *Vision Res* **32** 2165-75

Krauskopf J, Williams D R, Heeley D W, 1982 "Cardinal directions of color space" *Vision Res* **22** 1123-31

Lee D, Chun M M, 2001 "What are the limits of visual short-term memory: Objects or spatial locations?" *Perception and Psychophysics* **63** 253-257

Lovell P G, Tolhurst D J, Parraga C A, Baddeley R, Leonards U, Troscianko J, Troscianko T, 2005 "Stability of the color-opponent signals under changes of illuminant in natural scenes" *J Opt Soc Am A* **22** 2060-2071

Lucas P W, Dominy N J, Riba-Hernandez P, Stoner K E, Yamashita N, Loria-Calderon E, Petersen-Pereira W, Rojas-Duran Y, Salas-Pena R, Solis-Madrigal S, Osorio D, Darvell B W, 2003 "Evolution and function of routine trichromatic vision in primates" *Evolution Int J Org Evolution* **57** 2636-43

Luck S J, Vogel E K, 1997 "The capacity of visual working memory for features and conjunctions" *Nature* **390** 279-281

Liu J, Wandell B A, 2005 "Specializations for chromatic and temporal signals in human visual cortex" *J Neurosci* **25** 3459-68

Mackworth J F, 1964 "Auditory short-term memory" *Canad. J. Psychol.* **18** 292-303

Magnussen S, Greenlee M W, 1997 "Competition and sharing of processing resources in visual discrimination." *J Exp Psychol Hum Percept Perform* **23** 1603-1616

Marr D, Nishihara H K, 1978 "Representation and recognition of the spatial organization of three dimensional structure. " *Proceedings of the Royal Society of London B* **200** 269-294

Mullen K T, 1985 "The contrast sensitivity of human colour vision to red-green and blue-yellow chromatic gratings" *J Physiol* **359** 381-400

Mullen K T, Beaudot W H A, 2002 "Comparison of color and luminance vision on a global shape discrimination task" *Vision Res.* **42** 565-575

Oliva A, Schyns P G, 1997 "Coarse blobs or fine edges? Evidence that information diagnosticity changes the perception of complex visual stimuli" *Cognitive Psychology* **34** 72-107

Oostergaard A L, Davidoff J B, 1985 "Some effects of color on naming and recognition of objects" *J Exp Psychol Learn Mem Cogn* **11** 579-587

Parker A, Wilding E, Akerman C, 1998 "The Von Restorff effect in visual object recognition memory in humans and monkeys. The role of frontal/perirhinal interaction" *J Cogn Neurosci* **10** 691-703

Parkes L M, Marsman J C, Oxley D C, Goulermas J Y, Wuerger S M, 2009 "Multivoxel fMRI analysis of color tuning in human primary visual cortex" *J Vis* **9** 1-13

Parker D M, Lishman J R, Hughes J, 1992 "Temporal integration of spatially filtered visual images" *Perception* **21** 147-160

Pashler H, 1988 "Familiarity and visual change detection" *Perception & Psychophysics* **44** 369-378

Phillips W A, 1974 “On the distinction between sensory storage and short-term visual memory” *Perception & Psychophysics* **16** 283–290

Schyns P G, Oliva A, 1994 "From blobs to boundary edges: Evidence for time- and spatial-scale-dependent scene recognition" *Psychological Science* **5** 195-200

Schyns P G, Oliva A, 1997 "Flexible, diagnostically-driven, rather than fixed, perceptually determined scale selection in scene and face recognition" *Perception* **26** 1027-1038

Schyns P G, Oliva A, 1999 "Dr. Angry and Mr. Smile: When categorization flexibly modifies the perception of faces in rapid visual presentations" *Cognition* **69** 243–265

Sergent J, 1986 "Microgenesis of face perception", in *Aspects of Face Processing* Eds H D Ellis (Dordrecht: Dordecht: Martinus Nijhoff) pp 17-33

Shepard R N, Teghtsoonian M, 1961 "Retention of information under conditions approaching a steady state" *J Exp Psychol* **62** 302-9

Smithson H E, Mollon J D, 2004 "Is the S-opponent chromatic sub-system sluggish?" *Vision Res.* **44** 2919-2929

Sperling G, 1960 "The information available in brief visual presentations" *Psychological Monographs: General and Applied* **74** 1-30

Tanaka J W, Presnell L M, 1999 "Color diagnosticity in object recognition" *Perception & Psychophysics* **61** 1140-1153

Todd J J, Marois R, 2004 "Capacity limit of visual short-term memory in human posterior parietal cortex" *Nature* **428**

Vogel E K, Woodman G F, Luck S J, 2001 "Storage of features, conjunctions, and objects in visual working memory" *J Exp Psychol Hum Percept Perform* **27** 92-114

Wandell B, 1993 *Foundations of Vision* (Sunderland MA: Sinauer)

Waters A J, Gobet F, 2008 "Mental imagery and chunks: Empirical and computational findings" *Memory & Cognition* **36** 505-517

Wheeler M E, Treisman A, 2002 "Binding in short-term visual memory" *Journal of Experimental Psychology: General* **131** 48-64

Wichmann F A, Sharpe L T, Gegenfurtner K R, 2002 "The contributions of color to recognition memory for natural scenes" *J Exp Psychol Learn Mem Cogn* **28** 509-20