The Neural Networks Recruited During Visual Feature Binding

A dissertation presented by

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Abstract

The binding problem presents one of the most challenging questions in psychology and cognitive neuroscience, despite its seemingly effortless resolution in daily life. Binding of visual features begins with stimulation of peripheral receptors and ends with the emergence of a perceived object, yet many questions remain unanswered about the nature of the intervening mechanisms. The primary focus of this thesis was to elucidate neurocognitive processes that support binding of features into a coherent object. Experiment 1 sought to dissociate neural correlates of feature binding from spatial and temporal attention, which are frequently conflated in previous studies. Results showed a widespread network engaged during both forms of attention, without any significant clusters of activity in response to an explicit feature-binding task. One explanation for these results may lie in evidence that feature binding is a spontaneous process that happens implicitly upon observing an object. Therefore, in order to measure the network associated with implicit visual feature binding the established *reviewing paradigm* was employed in the subsequent studies.

Experiments 2 and 3 sought to replicate key aspects of the reviewing paradigm. The reviewing paradigm exploits the finding that when an object is shown in close spatial and temporal succession to another object it is perceived as a continuation of the same object. Therefore, if a feature changes between the initial object and the second presentation of this object then a rebinding of features occurs and a behavioural cost termed a partial repetition cost is often incurred.

In order to observe the impact of a relevant feature change compared with an irrelevant feature change, the reviewing paradigm was modified. Results indicated that an irrelevant feature change carried with it a reaction time (RT) cost almost as large as a RT cost observed following a relevant feature change. Experiment 4 aimed to observe the neural network recruited during the completion of the reviewing task experiment using fMRI and a whole brain analysis. Results showed a widespread network encompassing bilateral frontal and occipital areas. Furthermore, the network that was recruited during the irrelevant feature change condition was different from that engaged during the relevant feature change condition. In order to probe the causality of these actions, experiment 5 exploited the offline transcranial magnetic stimulation (TMS) to three key cortical areas: right lateral occipital complex, left superior frontal gyrus and left post-central gyrus.

The overarching conclusion of this thesis is that feature binding is an implicit and spontaneous process that is coordinated by a wider cortical network than expected from previous research. The parietal cortex has often been observed as the key area in which object representations become bound, however the results of this thesis do not support a unique or privileged role of this area in binding. The latter experiments show that feature binding is an interaction between the memory trace, action-based implications and perceptual demands of an object. How the brain co-ordinates this widespread cortical network during feature binding is a key question for future research involving TMS and brain imaging techniques.

Statements and Declarations

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My PhD was an unexpected opportunity. After a very surreal acceptance letter I began my PhD with huge excitement and expectation about my future. I have not been disappointed. The academic environment at Cardiff University is inspiring and nurturing, so for that I would like to thank all staff that have influenced my life while at Cardiff University. I'd also like to thank my supervisor Chris Chambers and my secondary supervisor John Evans.

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Table of Contents

Abbreviations

ANOVA: analysis of variance

ACC: Anterior cingulate cortex

cTBS: continuous theta burst stimulation

DLFPC: Dorsolateral prefrontal cortex

EPI: Echo Planar Imaging

FEAT: fMRI Expert Analysis Tool

fMRI: functional magnetic resonance imaging

FIT: feature integration theory

HRF: haemodynamic response function

HRT: haemodynamic temporal derivatives

IFC: irrelevant feature change

IFCC: irrelevant feature change cost

IFG: inferior frontal gyrus

IAS: implicit attentional selection

IPL: inferior parietal lobule

IPRC: irrelevant partial repetition cost

IPS: intra-parietal sulcus

ITG: inferior temporal gyrus

ITI: inter-trial intervals

LOC: lateral occipital cortex

MFG: middle frontal gyrus

MST: medial superior temporal area

MT: medial temporal

MTL: medial temporal lobe

NBP: neural binding problem

NC: no change (condition)

OC: occipital cortex

OSB: object specific benefit

PCG: postcentral gyrus

PFC: prefrontal cortex

PPA: parahippocampal place area

PPC: posterior parietal cortex

RFC: relevant feature change

RFCC: relevant feature change cost

rFEF: right frontal eye fields

rIFG: right inferior frontal gyrus

ROIs: Regions of Interest

RPRC: relevant partial repetition cost

SFG: superior frontal gyrus

SMG supramarginal gyrus

SPL: superior parietal lobe

STG: superior temporal gyrus

TMS: transcranial magnetic stimulation

TOJ: temporal order judgement

TPJ: temporo-parietal junction

VSTM: visual short-term memory

WBA: whole brain analysis

Chapter 1

Rationale and aim of thesis

The human retina transmits data to the brain at the rate of 10 million bits per second (Koch et al. 2006). Following transmission of this data, it must be selected and integrated. Although the human visual cortex is arranged in a modular fashion, with different types of visual information processed in distinct cortical areas (e.g. colour in area V4 and motion in area MT), we perceive a cohesive scene. How the brain integrates accurately this disparate visual information to represent the environment is termed the *binding problem*.

Di Lollo (2012) proposed that the neural binding problem (NBP) encompasses at least four distinct components: coordination, subjective unity of perception, variable binding, and visual feature binding. The latter point of the NBP, visual feature binding, is the focus of this thesis. Visual feature binding refers to the process in which different features such as shape, colour, size, orientation and location, are integrated to form a coherent representation of an object, collections of which comprise the scenes we encounter on a daily basis.

Although binding has been postulated to underpin a host of cognitive functions, from perceptual processing of objects and their constituent elements (Malsburg, 1981) to higher order cognitive processes such as memory and reasoning (Halford, Cowan, & Andrews, 2007), visual feature binding is an essential element of information processing, providing the basis of mental representations, which in turn are pre-requisites for all cognitive processes. Understanding the neural substrates of visual feature binding, therefore, may provide greater insight as to how this process may serve more complex, higher-order cognition.

This thesis employs experimental psychology, neuroimaging and transcranial magnetic stimulation (TMS) to probe the cortical network recruited during the process of visual feature binding. The main context for this thesis is work carried out by Kahneman, Treisman, and Gibbs (1992) and more recently by Hommel (1998) and Hommel, Proctor and Vu (2004). These studies used a behavioural paradigm known as the 'reviewing paradigm’ (details provided below) to evoke rebinding or an updating of a bound stimuli.

This thesis begins by investigating the neural network engaged during explicit feature binding. Following this, I examine the brain regions engaged during the reviewing paradigm (Kahneman, Treisman & Gibbs, 1992), which is assumed to reflect the process of rebinding. In the following sections of the Introduction, I will review the literature relevant to visual feature binding, before providing a brief overview of the experiments outlined in this thesis, and the questions that they aim to address.

1.1 General introduction

"Every perception is an act of creation" – Gerald Edelman (2006).

Vision is initiated via the detection of light on the retina and culminates in an experience of our environment that has a movie- like quality. However, between light hitting the retina and the phenomenological experience of 'seeing', a visual representation of the world is constructed.

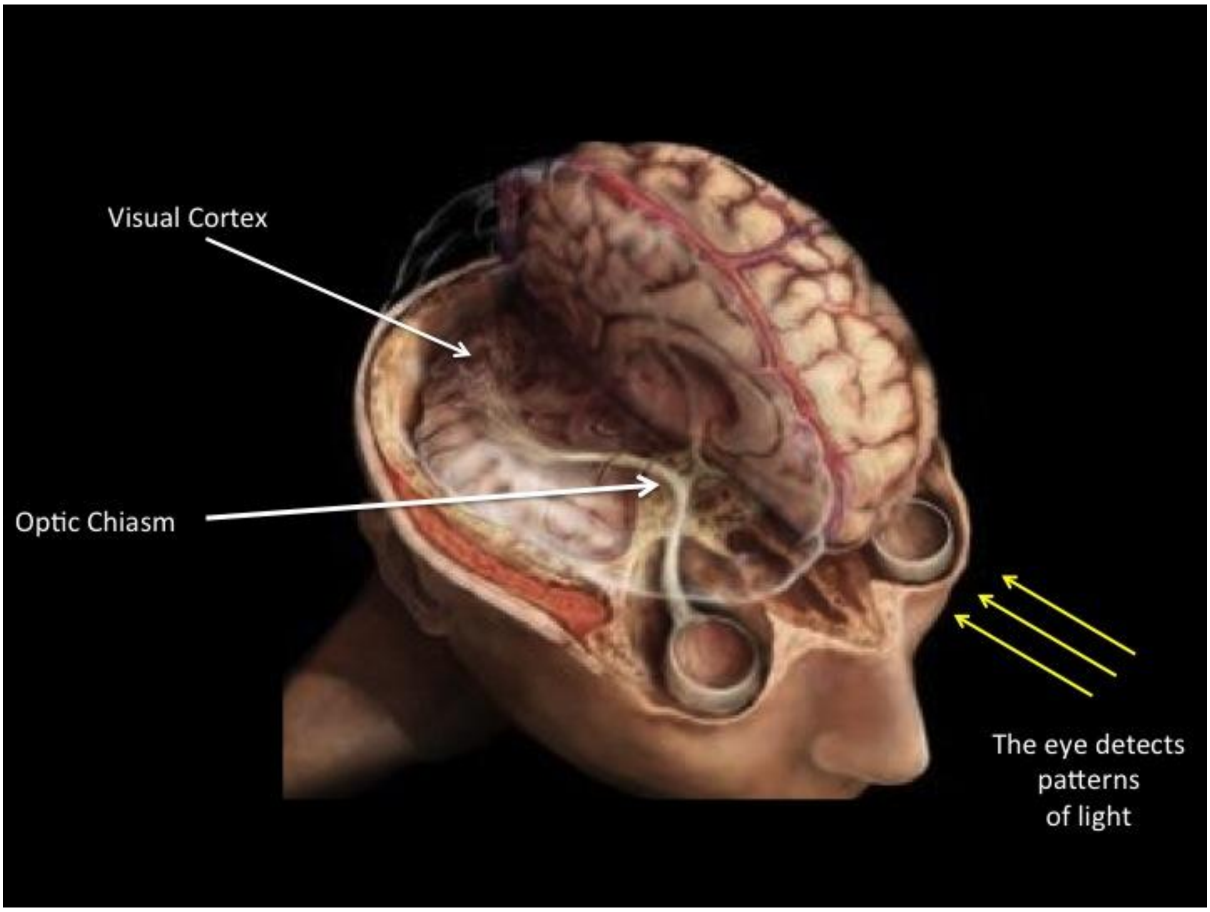


Figure 1.1. The eye receives information in the form of light; information is then transmitted to the visual cortex where a representation of the environment is constructed (adapted from http://www.superior-view-of-the-brain.co.uk).

Much research has taken place in order to elucidate how the brain reconstructs the world around us, and it has been posited that a process integral to this reconstruction is ‘feature binding’. My thesis examines the neural networks engaged during feature binding and therefore I will begin with a review of the literature surrounding the feature binding problem and the models that have been proposed as a solution.

1.2 The Feature Binding Problem

Feature binding concerns how different features of an object are brought together to form a coherent and accurate object representation (Treisman, 1998). The ‘problem’ relates to the as yet unanswered question of how anatomically distributed patterns of neural firing result in a coherent and veridical representation of the immediate environment.

Conscious experience of the environment does not consist of disembodied features; rather, it comprises unified objects and their backgrounds (Treisman and Schmidt, 1982). This perceived cohesion of the environment belies the fact that the brain is performing a large-scale integrative process within milliseconds of receiving information from the retina. Some of the strongest evidence that the brain is solving the binding problem is evidenced when the binding process fails. The outcome of mis-binding is a phenomenon called ‘illusory conjunctions’. An illusory conjunction occurs when a subject has accurately perceived the individual features that are present in a display, but has conjoined them incorrectly. For example, if the display consists of a red circle and a blue square, the subject might report a blue circle and a red square. I shall return to the discussion of illusory conjunctions later in the chapter, and their relevance in helping us to understand the ‘binding problem’.

Malsburg (1981) proposed one of the first models to explain how the brain solved the ‘binding problem’ and postulated that neural synchrony may be the mechanism by which information is bound together. This notion received support from Singer and Gray (1995), who suggested that binding is achieved by transient and precise synchronisation of neuronal discharges as seen in the cat striate cortex (Gray, Engel, Konig & Singer, 1992). The idea of synchrony assumes that, as binding occurs throughout the brain, synchronous firing of cortical neurons leads to the binding of features. Although oscillation between out of phase firing has been proposed as a possible mechanism to encode separate objects, it is difficult to imagine how such a precise timing mechanism is possible, considering the amount of objects that are the visual system is presented with at multiple locations (Jaswal, 2012). Although it is likely that the synchronisation of neuronal firing plays a role in the binding process, a more comprehensive theory, the feature integration theory (FIT), garners support from a number of converging paradigms and has become the most viable framework in which to explain the feature binding process (Treisman, 1985; Treisman & Gelade, 1980; Treisman & Schmidt, 1982).

The FIT argues that features are bound together by selectively attending to a location. Following this, features that fall within the attended space then become bound into an object. Therefore, the FIT consists of two stages; the first stage is the pre-attentive stage. At this stage perception is proposed to occur automatically and unconsciously. The object is analysed for details such as shape, colour, orientation and movement, with each feature being processed in different regions of the brain. The second stage of the FIT is the focused attention stage. During this stage, a location is selected and the features within this location become bound into an object. In order to do this, the FIT proposes that there is a master map of locations, which details the location of all features that have been detected within the visual scene. As shown in figure 1.2, once attention has then selected a location, the features within that location become bound.

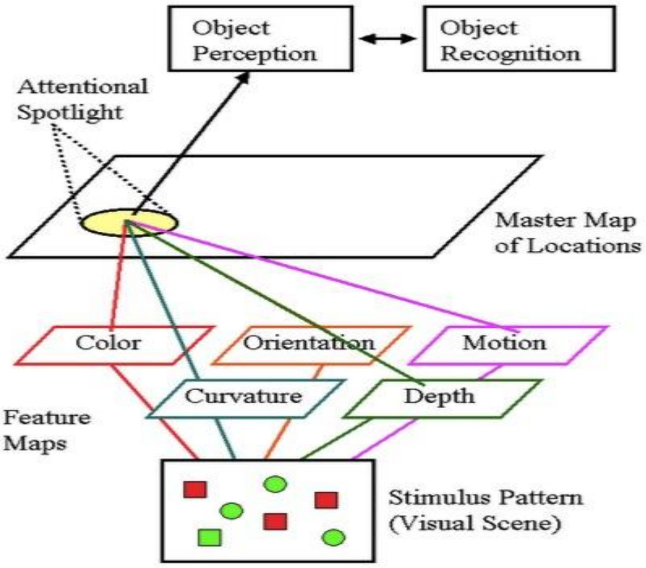


Figure 1.2 shows the premise of the FIT. In order to perceive an object a person would selectively attend to a location. All features within that location become bound to that location in space. Image taken from http://www.luc.edu/faculty/asutter/FIT.html.

If the predictions of the FIT are correct, and selective spatial attention is the mechanism by which features become bound, then one would predict that if spatial processing became compromised then binding errors would be observed. This is what is observed in both patient studies and through the phenomenon of illusory conjunctions. I will discuss these below.

Much evidence in favour of the FIT has come from the experience of illusory conjunctions. Firstly, IC's are commonly seen when exposures are brief and focused attention to each object in turn is prevented. Second, directing attention in advance to the location of a target improves identification more for conjunctions that for simple features (Tresiman & Schmidt, 1982). However, whether these are direct effects on binding or an indirect result of attention being allocated to perceptual groups of elements is not clear.

Further evidence in favour of the FIT, and the assertion that selective spatial attention is necessary to bind features together, comes from clinical case studies of patients who have Balint's Syndrome. Balint's syndrome is often seen following the damage of both parietal lobes; patients can lose the ability to process spatial information about the environment around them. As stated by Homles and Harax, (1919): the three main symptoms that characterise the disease are simultanagnosia (inability to see more than one object at a time); optic ataxia (the fixation of gaze with severe problems in voluntarily moving fixation); and optic apraxia (the inability to reach towards the correct location of perceived objects). Although patients can see one object at any given moment, they do not know where it is located; it is as if there is features do not belong to anyone location within the visual field, due to this patients often report the features jumping from one location to another (Robertson, 2003). The FIT predicts that spatial information is the medium through which the brain binds features together. Therefore, if the brain no longer computes a spatial map, then features should no longer become bound into objects. However, as stated by Friedman-Hill et al. (1995) - in order for the deficit to be binding specific, patients should still be able to accurately detect individual features present across the visual field.

In order to test these predictions a series of experiments were carried out with patient R.M (Freidman-Hill, Robertson & Treisman, 1995). R.M. suffered nearly symmetrical bilateral parietal lesions, with no temporal or frontal lobe involvement, as a result of two strokes. Although R.M. did not exhibit an attentional bias for the left or right visual field, he did have great difficulty reporting where objects were located, even after directing his gaze to them. This allowed Friedman-Hill et al. (1995) to investigate the effects of degraded spatial information on feature binding. In order to test R.M's ability to bind features, he was presented with a display containing two coloured letters. His task was to report the name and colour of the first letter he saw. The results showed that R.M. had an illusory conjunction rate of 13%, even when the display times were as long as 10s per trial. A further observation was the R.M made significantly more errors when stimuli were presented simultaneously, rather than when the coloured letters were presented sequentially. This was apparent even though the display time was twice as long in the simultaneous condition than in the sequential condition. This data suggests that R.M. was able to bind features using the temporal information (sequential order) to distinguish items, but showed specific spatial processing deficits when attempting to bind features together when several objects were present across the visual field. This implies that rather than showing a deficit in the ability to bind per se, as argued by Treisman et al. patients with Balint's Syndrome demonstrate a specific impairment in spatial processing, which indirectly effects accurate feature binding (Robertson, 1999).

The network recruited during spatial attention has been identified through convergent findings from neuropsychological and brain imaging studies (Corbetta, Miezin, Shulman, & Petersen, 1993; Nobre et al. 1997). The core brain regions comprising this network are the posterior parietal cortex (PPC) near the intra-parietal sulcus (IPS), frontal eye fields (FEF), lateral and medial premotor cortex (PMC), anterior cingulate (AC) and sub-cortical areas such as the thalamus and the striatum (LaBurge & Buchsbaum, 1990; Corbetta, Patel, & Shulman, 2008; Nobre, Coull, Walsh, & Frith, 2003).

Neuropsychological studies show robust evidence that damage to both right parietal cortex and frontal cortex can give rise to neglect of visual stimuli in the contralateral hemi-field (Bisiach et al. 1984; Damasio et al. 1980; Mesulam, 1981), a syndrome that is linked to deficits in orientating spatial attention (Mesulam, 1999). Neglect can even be induced in healthy participants by inhibiting the contra-lateral parietal cortex using TMS (Bjoertomt et al. 2002; Fierro et al. 2000).

Functional neuroimaging studies of healthy participants provide further evidence that a large-scale distributed network, including bilateral parietal and frontal cortex, are involved in orienting spatial attention to both the left visual field (LVF) and right visual field (RVF) (Corbetta et al. 1993; Han et al. 2004; Yantis et al. 2002). Recent research has shown that distinct regions in the fronto-parietal network are engaged in different aspects of attentional control such processing of cues and attentional orienting (Woldorff et al. 2004).

As a key cortical area within the spatial attention network, PPC has long been regarded as a candidate structure to house the master map of locations, a key component in the second stage of feature binding, as proposed by the FIT, (Treisman, 1998). The most compelling evidence for a contribution of PPC to feature binding comes from patient studies previously discussed (Friedman-Hill et al. 1995; Humphreys, 2001). However, in many fMRI studies a visual search paradigm is often used employed, as the task is well suited for investigating both spatial attention and feature binding. The visual search usually entails an active scan of the visual stimuli in order to identify a target among other objects and features. However, neuroimaging and TMS studies are yet to conclusively show a role for the PPC specifically in feature binding, rather than in processes such as search efficiency, which one would expect to be taxed during a visual search paradigm.

Using a visual search paradigm, some neuroimaging and lesion studies in humans provide support for the role the PPC in feature binding, for example a PET study reported activation in PPC during a feature conjunction search, but not during easy visual searches for single features (Corbetta et al. 1995; Corbetta and Shulman, 1998; Robertson, 1998; Treisman, 1996). These results are also supported by the observation that following repetitive transcranial magnetic stimulation (rTMS) over the PPC a visual search for a conjunction of features was impaired whereas an easy feature search was not (Ashbridge et al, 1997). Furthermore patients with bilateral PPC lesions have been reported to mis-bind object features (Friedman-Hill et al. 1995; Humphreys et al. 2000). However, as previously discussed there is also evidence that the involvement of the PPC in visual search may not be binding specific but may reflect a more general attentional mechanism. Therefore, in summary, although the PPC may facilitate binding, it has been difficult to rule out that this region plays only an indirect role in binding by supporting visual search.

In order to explore further the role of the parietal cortex in visual feature binding Shafritz, Gore and Marois (2002) conducted an fMRI study in which subjects had to complete a change detection task. In this task, subjects were required to determine whether a test object matched either of two previously presented sample objects with regards to its shape, colour or combination of shape and colour. The stimuli consisted of 5 novel geometric shapes, and sample objects were presented either simultaneously or sequentially. The analysis used a previously defined region of interest (ROI) in the right parietal cortex that had shown preferential activation for location judgement activation – the anterior intra-parietal and superior parietal cortex. They also used an identical ROI for the left parietal cortex. In order to avoid the pitfalls of directly contrasting simultaneous and sequential presentations the conjunction conditions was compared to its respective single feature condition, as these were physically matched. This meant the effects of feature judgement (colour/shape/conjunction) and presentation mode (simultaneous /sequential) were assessed separately in the right and left parietal ROIs. The results showed that when the objects were presented simultaneously, there was greater associated activity in the parietal cortex, compared to when subjects performed the same conjunction task but with the stimuli was presented sequentially. Shafritz et al. (2002) concluded that the parietal cortex is engaged when spatial, but not temporal, cues can be used to resolve binding ambiguity.

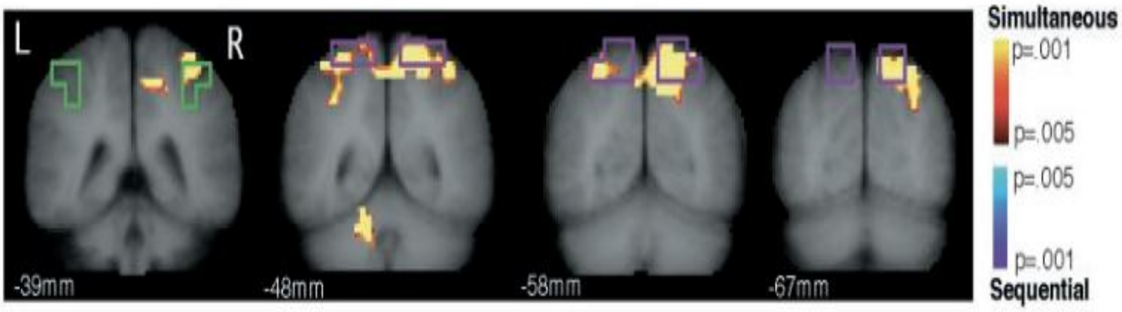


Figure. 1.3 Direct comparison of conjunction related activation in the simulataneous (yellow) and sequential (blue) presentations. The green and purple boxes indicate the position of the intra- and superiror parietal ROIs, respectively (Taken from Shafritz et al. 2001).

However, the observation that the parietal cortex, specifically the superior parietal cortex, has shown robust retinotopic qualities, may explain the increase in BOLD in this area when objects were presented simultaneously as opposed to sequentially. (Sereno, Pitzalis & Martinez, 2001). Differences in lower-level perceptual features of the stimuli, therefore, could explain the pattern of data observed in this study.

In an attempt to establish the role of the parietal cortex in feature binding, Nobre, Coull, Walsh and Frith (2002) employed a visual search paradigm alongside functional MRI. There were four visual search tasks in which Nobre et al. (2002) manipulated: i) the requirement to either integrate features prior to a visual search task or the requirement to carry out purely a feature detection task (feature or conjunction search) and ii) the degree of search efficiency (efficient or inefficient). The aim of the experiment was to tease apart the contribution of search efficiency versus feature binding to brain activations during visual search. Subjects performed four visual search tasks in a single experimental session. In order to assess whether the search performed was efficient or inefficient reaction time was measured. If reaction time remained constant the search was classified as efficient, whereas if the reaction time increase progressively they were classed as inefficient. When contrasted to the efficient feature detection condition, the efficient conjunction condition enabled the identification of brain areas sensitive to feature binding without increasing target-selection demands. Nobre et al. (2002) found that all search conditions activated an extensive cortical network including the bilateral parietal cortex, superior and inferior parietal cortex as well as the IPS. One contrast of interest was that comparing the inefficient search for conjunctions with efficient search for features. In this comparison, the factors of efficiency and binding are conflated. In this contrast Nobre et al. observed significant enhancement of parietal activation in the inefficient search for a conjunction compared to the efficient search for a feature. To tease apart areas engaged in binding as opposed to search efficiency the following contrast was calculated (efficient conjunction-efficient feature) + (inefficient conjunction-inefficient feature). Following this contrast, in which the activity related to search efficiency was controlled, results showed that feature binding exerted only sparse direct effects on brain activations. No brain region was selectively activated by conditions requiring binding of different types of features and no other brain regions showed any effect of feature binding conditions. However, the conclusion that parietal areas are not involved specifically in feature binding is based on a null result: there is a lack of a BOLD response to feature binding which is independent or different from the BOLD response to search efficiency.

Inconsistencies in data, not only result from the use of different paradigms but also different statistical analysis methods. A more recent study (Baumgartner et al. 2013) employed multi-variate pattern analysis (MVPA), as opposed to the commonly used univariate analysis, and aimed to directly investigate location-specific representations of feature conjunctions, in which two (or more) features from different visual dimensions, were represented together with their exact locations in the visual field. In order to do this, Baumgartner et al. (2013) showed a display consisting of 5 coloured gratings. Between trials either the spatial frequency of the grating, colour of the grating, or a combination of the two, was varied at a specific location on the display. MVPA was then used to classify activation patterns elicited by colour changes, spatial frequency changes, or changes of both colour and spatial frequency. The hypothesis was that if only colour or spatial frequency changes between two displays, their classification relies on feature detectors (neurons that are processing either colour or spatial frequency) alone. If both features change, however, classification could rest on conjunction detecting neurons, or alternatively the additive effects of colour detectors and spatial frequency detectors. The results showed that the right anterior superior parietal lobule showed higher classification accuracy for location-specific conjunctions of colour and spatial frequency than for either component features in isolation or their average. The cortical location of the conjunction of colour and spatial frequency was in the superior parietal lobule. Although the parietal cortex is consistently associated with feature binding, the precise cortical region activated within the parietal cortex is inconsistent across studies. An explanation for this maybe down to the differing task requirements; that is, the neural substrates are functionally heterogeneous depending on the paradigm employed, this may also be due to the diverse statistical contrasts employed across fMRI studies.

In direct contrast to these results, it has recently been demonstrated that the neural signature of feature binding is present much earlier in the visual processing stream than previously thought. Using MVPA, Seymour and Logothetis (2010) demonstrated that feature conjunctions are represented already in early visual cortices (Seymour et al. 2009, 2010).

A possible explanation for this contradiction, as suggested by Baumgartner et al. (2013), could be that their study was focused on the parietal cortex and was not optimally suited to investigate feature binding in occipital cortex. However, the results are not mutually exclusive and it is likely that the formation of feature conjunctions is dependent upon re-entrant connections between the parietal and occipital cortices (Treisman, 2006). This theory is supported by studies carried out with patients with parietal lesions (Friedman-Hill et al. 1995) and healthy occipital lobes. These case studies have shown preserved processing in the occipital cortex is not sufficient to result in consciously perceived feature conjunctions across the visual field.

As discussed earlier in the chapter, when patient R.M. was unable to use spatial information to bind features together during simultaneous presentations of coloured letters, sequential presentation of the coloured letters allowed R.M. to use temporal information to bind features together which resulted in an increase in accurate feature binding reports. The role of temporal attention in feature binding is relatively unexplored, this is something I look to address in the first experimental chapter (Chapter 2), therefore I summarise the relevant literature below.

Although attention is distributed in time as well as space, temporal attention is a relatively neglected area of research in comparison to spatial attention. However, temporal attention influences and facilitates behaviour in a similar way to spatial attention. If spatial attention is cued to a specific location we are quicker to react to changes at that location, for example, we are quicker to accelerate away from a traffic light if our spatial focus of attention is directed towards the location of the green light, rather than towards a nearby shop window (Coull, 2004). Similarly, if our attention is cued to a time window in which changes are expected to occur our reactions are faster. Although not as well researched as spatial attention there have been several fMRI studies that have investigated the interaction between attention and time using two complementary approaches. Nobre and Coull, (1998) carried out one the of the first fMRI studies which aimed to reveal the brain regions involved in directing attention towards a particular point in time instead of a particular point in space. In order to investigate this question, Nobre et al. (1998) developed a task that is known as the temporal analogue of the spatial orientating of attention task developed by Posner (1980). In the spatial version of this task, subjects respond as quickly as possible to visual targets appearing at peripheral locations. Immediately preceding the target is a cue that either correctly (“valid cue”) or incorrectly (“invalid cue”) predicts the location of the upcoming target. In the temporal version of this task, subjects respond as quicly as possible to the target which is preceded by either a valid or invalid cue which predicts the temporal moment the stimuli would appear. This tested the hypothesis that stimuli that occurred at predicted intervals were detected more quickly than those that did not appear at the predicted intervals (see Figure 1.4 below). Nobre et al. (1998) used both fMRI and PET in order to visual the neural network engaged during temporal attention versus spatial attention.

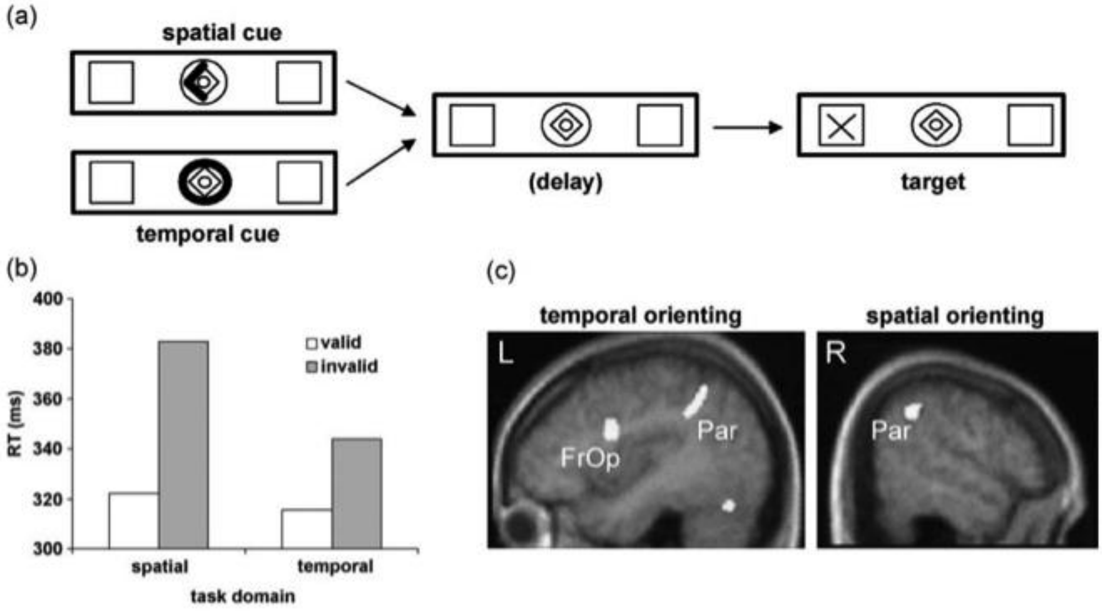


Figure 1.4 The visual display consisted of a central cueing stimulus and two peripheral boxes inside which the target appeared. The subjects task was to explicitly detect the peripheral target stimuli as rapidly and as accurately as possible. The task manipulated subjects' expectations of *where* or *when* target stimuli would appear within an experimental display. A, attentional cues used to direct subjects' attention to a particular target location or stimulus-onset time. The neutral cue provides neither spatial or temporal information, the spatial cue directions attention to the left or right, the temporal cue directs attention to a short or long stimulus-onset time, and a space-time cue directs attention to both a location and stimulus onset. B,Performance was slower for invalid spatial and temporal cues. C, hemispheric lateralisation in the left an right parietal cortex for temporal and spatial orienting, repectively. (Taken from Coull, 2004).

The fMRI analysis compared each condition (spatial, temporal and spatial-temporal) to a resting baseline. Contrasting the spatial condition with baseline resulted in increased BOLD response in the right IPL, left occipital-temporal sulcus and left cerebellum. In contrast, relative to baseline the temporal condition was associated with left IPS, left lateral inferior premotor cortex and left cerebellum BOLD signal. Carrying out both tasks combined led to an increase in BOLD in the right TPJ, right IPS and left IPS.

The right hemisphere bias for spatial orienting in the study is consistent with previous studies (Corbetta et a. 1993; Nobre et al. 1997). Finding a left hemisphere bias for temporal orienting was a novel finding. However, in this experiment the subjects were significantly faster completing the temporal task than the spatial task, perhaps reflecting differences in task difficulty that may have confounded the analysis.

On the basis of the inconsistencies across studies, experiment one of this thesis aimed to contrast the neural networks recruited during a spatial, temporal and feature binding task while controlling task difficulty and low-level stimulus differences. The aim was to identify whether there were any cortical areas that were specifically engaged during feature binding above and beyond those engaged during spatial and temporal attention.

So far the literature discussed has focused on the cortical engagement during explicit feature binding. However, in recent years, many dissociations have been observed between conscious (explicit) and non-conscious (implicit) processing of visual information in neurological disorders, such as unilateral neglect or simultanagnosia. Brain damaged patients often possess high-level visual knowledge of which they are unaware. Berti and Rizzolatti (1992) showed that patients with neglect denied that an object is present in the contra-lesional visual field, and yet show semantic priming from that object. This is supported by further studies that were carried out with patient R.M. (Wojciulik and Kanwisher, 1998) that are discussed below.

Following bilateral parietal damage, Friedman-Hill et al. (1995) found that R.M made an abnormal number of ICs between colours and shapes when asked to explicitly identify coloured letters. It was argued that this was evidence that the binding mechanism has been disturbed due to the loss of the ability to process spatial information and therefore use the ‘master map of locations’ to bind features. However, despite this, Wojciulik and Kanwisher (1998) demonstrated that R.M was sensitive to Stroop interference, suggesting that colour and form information was bound together, at least at some stage. In order to demonstrate this, Wojciulik et al. (1998) presented two words one above the other, on a black background. One word was coloured and the other was white. The task was to name the non-white colour as quick as possible. There were two conditions named same object consistent (SOI) and different object inconsistent (DOI). In the SOI condition, the colour-name word and the colour of the word was inconsistent (for example, the colour name was purple and the colour of the word was green); the white word was consistent with the colour of the word (for example the white word would say green). In the DOI condition, the white word was inconsistent with the colour, and the coloured word was consistent between the name and colour (for example, the white word was purple; the coloured word had a matching colour and name – e.g. green name and green colour). The results showed that R.M was slower to name the colour in the SOI condition that in the DOI condition. Within the same study, R.M was then asked to read the coloured word (colour neutral words were used). The latter task required R.M to have explicit knowledge of which word was bound with which colour, where as the former task tested whether there was any implicit knowledge of the binding between the word and colour of the word presented. As in previous explicit binding studies, R.M performed at chance; he was just as likely to read the word in white as the coloured or non-white word. Several other studies have demonstrated implicit binding in patients with parietal damage and poor explicit binding (Ridoch, Nys & Heinke, 2002; Cinel & Humphreys, 2006).

Furthermore, several studies in healthy subjects have shown that viewing a stimulus can lead to automatic and spontaneous binding that in turn modulates subjects RT to a single feature within the visual field (Melcher, Papathomas and Vidnyanszky, 2005). Further evidence of implicit feature binding has been demonstrated following the completion of a reviewing paradigm, which is highly relevant to the remaining experiments in this thesis and therefore explored in the section below.

1.3 Implicit feature binding and the formation of object files

Experiment 1 (Chapter 2) focuses on the processes involved in conscious explicit selection of task relevant sensory input, and differentiating between the neural networks engaged during either an explicit spatial, temporal or feature binding task. However, there is much evidence for implicit feature binding that is both spontaneous and automatic. Therefore, in experiment 2a, 3, 4 and 5 I explore the implications and after-effects of implicit feature binding. In the rest of this chapter I discuss the most relevant literature surrounding the formation of objects and the implicit spreading of attention across features in the visual field.

Previous experiments have demonstrated that directing attention to a specific colour of an object results in attentional modulation of the processing of task-irrelevant features. Melcher et al. (2005) carried out a seminal study in which the implicit spread of attention was examined. The results showed that implicit cross-feature spreading of attention takes place according to the veridical associations between the colour and motion signals (Melcher et al, 2005). These results were observed following the employment of a novel paradigm in which Melcher et al. (2005) tested whether global attentional selection affects other, task irrelevant features of unattended objects that share the attended feature. Further to this they looked to elucidate whether implicit attentional selection is determined by early feature binding that is based on the spatiotemporal correlation between different features or a binding mechanism that links features that belong to the same perceptual object.

Their results showed that implicit attentional modulation spreads to task irrelevant features that are spatiotemporally inked with the attended features throughout the field, meaning that the binding is based on the veridical physical associations between the features rather than a binding mechanism that relies on the linking features that are part of the same perceptual object. This is different from explicit attentional selection inside the focus of attention (Sohn et al. 2004).

Furthermore, it has been shown that implicit associations can continue to modulate RT for up to 4 seconds. A mechanism by which the product of feature binding is preserve products of the feature integration process, has been proposed by Kahneman, Treisman and Gibbs (1992).

Building upon the FIT, Kahneman et al, (1992) proposed the 'object file theory' in which they assume that the result of the integration process is temporarily stored in what they call an "object file". Object files are proposed to contain information of the feature conjunctions of the corresponding object, together with information about the current object location. Kahneman et al, (1992) suggest that once formed, object files keep track of objects, in spite of changes in their features over time.

The object file theory suggests that the visual field is separated into perceptual objects and a relatively undifferentiated perceptual background. It is then assumed that the end product of perceptual processing is a number of object files, with each object file containing information about a particular object in the scene. A key assertion of the object file model, as proposed by Kahneman et al, (1992), is that an object file can only be addressed by its location at a particular time, not by any non-spatial feature.

Therefore, when changes occur, current information about the changing or reappearing objects must be assigned to the existing object files; if this fails a new file must be set up. This is also a mechanism through which the visual system is proposed to provide perceptual continuity throughout change. Kahneman et al. (1992) argue that three distinct operations are needed to provide perceptual continuity throughout change: (i) a correspondence operation determining whether the object is “new” or whether it is an object recently perceived, now at a different location; (ii) a reviewing process retrieves the characteristics of the initial object, now no longer in view; (iii) a completion process that uses current and reviewed information to produce a percept of change or motion that links the two views. In order to test their theory Kahneman et al. (1992) developed the reviewing paradigm.

The reviewing paradigm consists of two successive displays, labelled the preview field and the target field, respectively. In this paradigm, the preview field contains two or more different letters. Participants were then presented with the target field containing a single letter, which the participant was required to name as quickly as possible (RT was recorded in this task). There were three conditions: (i) same object - when the target letter matched any one of the preview letters in both form and location; (ii) different object -when the target matched one of the preview letters in form but not in location; (iii) and no match - when the target did not match the preview letters in either form or location.

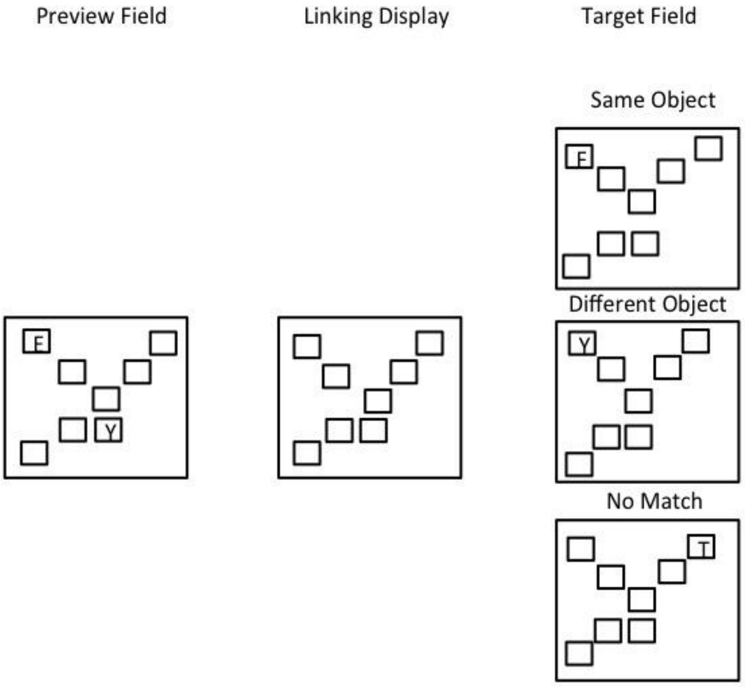


Figure 1.5 Examples of displays used in Kahneman et al. (1992) object file paradigm. The three headings (Preview Field, Linking Field and Target Field) show three successive displays, shown at different time intervals . The headings above each screen under Target Field in each case show examples illustrating the three main relations between the previous field and the target field, taken from Kahneman et al. (1992).

In summary the results showed that if the letter that appeared in the target display was already part of the prime display the responses we significantly faster than when there was no match between the probe and prime letters, Kahneman termed this a non-specific benefit. However, this preview effect was also much larger when the matching letter appeared in the same location as the previous letter, this was termed the object preview effect. On this basis, Kahneman et al. (1992) assert that the identity of the prime letter and the location of the prime letter are integrated into letter-specific object files. If both the location and form of the letter repeat then an "object specific preview benefit" was seen. However, if the location did not match but the letter did, Kahneman et al. (1992) observed a much weaker "non-specific preview benefit". Non-specific preview effects have different theoretical implications (Hommel, 1998). Non-specific effects are usually attributed to the priming of “type” representations; that is, stored descriptions of object features in long-term memory. It is proposed that each feature is represented by one neural code or representation, so that, if a feature is shared by more than one object in the field, the activation of a code does not unambiguously identify its source, meaning that ‘retrieval’ is not triggered. Object-specific effects, as observed in negative priming and preview tasks, imply that encountering a visual event does not only result in the priming of object types, but also in separate episodic bindings of the features belonging to the objects perceived.

In order to explore object files further, the reviewing paradigm structure was employed in several experiments carried out by Hommel (1998). In these experiments participants performed a binary-choice task in response to the shape of a stimulus (termed S2) that was preceded by another stimulus (termed S1), the features of which were irrelevant. Unlike the paradigm that Kahneman et al. (1992) had designed, the experimental design allowed for an independent manipulation of the shape, location, and colour of the stimulus between presentation in S1 and S2, so that performance could be compared across either a no match, complete match or a partial repetition. The effects of feature repetitions were not independent of each other: repeating shape produced better performance than alternation, only if colour was also repeated, but worse performance than alternation if colour alternated; the same relationship was observed between shape and location. Hommel (1998) argued that given that complete matches led to about the same performance as mismatches, these results did not point to a benefit of repeating a particular feature conjunction (object specific benefit), as interpreted from by Kahneman et al. (1992).

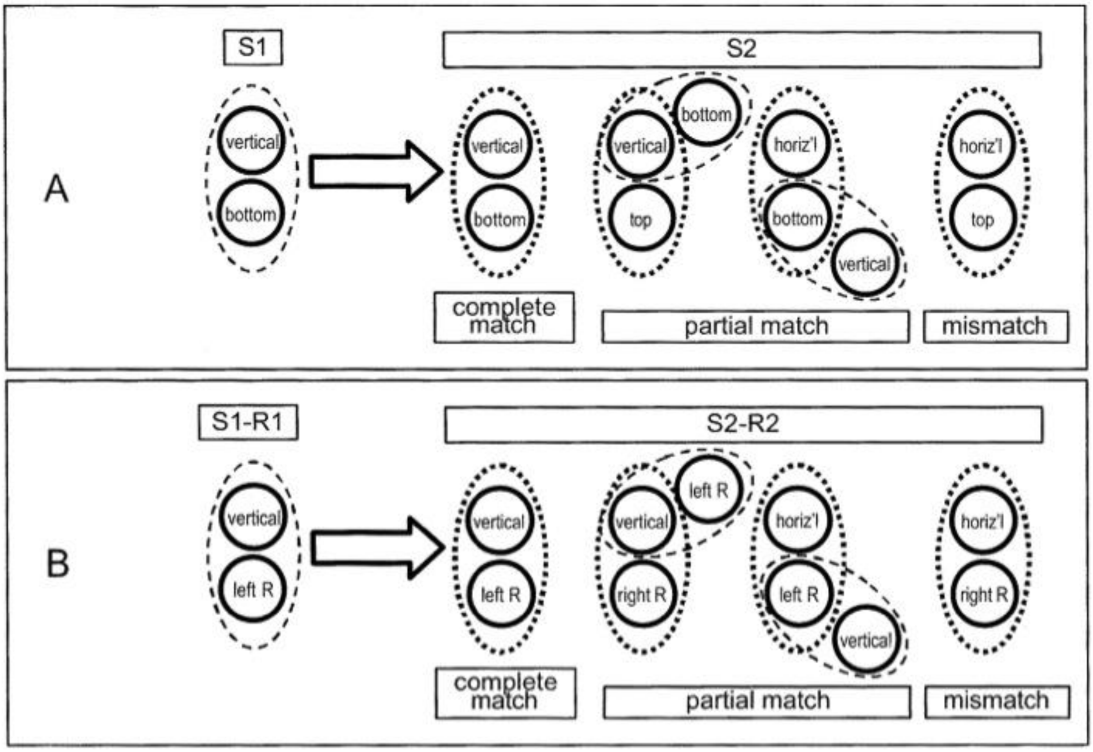


Figure 1.6 A binding account of partial repetition costs. (A) The assumption is that feature codes representing stimulus 1 (S1) are temporally integrated into a coherent event file. If relations between the features within this event file completely match or completely alternate then these bindings and reaction time performance is unaffected. However, if there is a partial repetition leads to the recall of incorrect event files which led to conflict and hence leads to a slower performance. The same logic applies when a response (R1) is integrated with S1 (B). Taken by Hommel and Colzato (2004).

These data suggested that instead of an object specific benefit, what was being observed was in fact a partial repetition cost. It was further demonstrated that the contents of object files were not restricted to just stimulus features. Following the adaptation of the reviewing paradigm (Figure 1.4 - B), participants were required to make a speeded button press on viewing the initial stimulus (S1 - left R or right R in Figure 1.4). Subjects were told that this response was unrelated to the stimulus and not relevant to the response required during S2. This modification enabled Hommel (1998) to observe whether the response that arbitrarily co-occurred with the onset of S1 became bound with the features of S1. The relationship between the motor response required during S1, and the motor response required during S2, was then examined in order to assess whether partial repetition costs were present when the motor action alternated between S1 and S2, as opposed to when it repeated, and furthermore whether this interacted with the partial repetition of stimulus features. The results showed that the repetition or alternation of stimulus features also interacted with response repetition. For example, response repetitions were faster and more accurate if stimulus shape was also repeated than if shape alternated, whereas response alterations were faster and more accurate if shape alternated rather than repeated.

In experiments 2a 3, 4 and 5 of this thesis, I adapt the reviewing paradigm in order to differentiate a partial repetition cost caused by the alteration of either a task irrelevant feature or a task relevant feature. In order to do this two partial repetition costs are calculated with two separate baselines. This also allowed me to control for a motor switch cost that may be confounding the RT observed in trials in which the task relevant feature alternates. Further, in order to explore the limitations of object files, experiment 2B explores whether object files exist on a purely perceptual level; that is, whether conceptual information is integrated automatically along with the perceptual features, or whether conceptual information is something that would become integrated over time and stored in long-term memory structures. The literature surrounding the integration of semantic information is discussed in more depth in Chapter 3.

1.4 The neural correlates of object files

A single study has previously combined the reviewing paradigm with functional neuroimaging (Keizer, Colzato and Hommel, 2008) and the stimuli used in this experiment were already complex, specifically houses and faces. In order to expand the limited literature that addresses the cortical areas engaged during the formation of object files, and possibly feature binding, experiment 4 of this thesis combines the reviewing paradigm with fMRI. However, unlike the experiments discussed below, experiment 4 of this thesis uses simple stimuli in order to avoid the possible confounds of using already complex stimuli such as houses and faces. I will discuss the current literature surrounding the neural correlates of object based attention and object files below.

According to the integrated competition model, directing attention to one feature of an object enhances neural activity in the cortical module encoding that feature, which then spreads to different modules that encode the other features of the object. This results in activation of the entire network of specialised modules. This process is suggested to underlie the binding of features of the attended object into a unified perceptual experience. This model was extended in the incremental grouping model (Kanwisher, McDermott & Chun, 1997) which proposes that feature binding involves the spread of enhanced neural activity, across the network of visual areas, that encode the features of an object. It is thought that this is achieved via re-entrant connections between the occipital and parietal cortices (Schoenfeld, Hopf, Merkel, Heinze, Hillyard, 2014, Bouvier &Treisman, 2010).

A key prediction of object-based theories is that directing attention to a particular feature of an object, such as its shape or colour, results in the whole object being selected, including both task relevant *and* task irrelevant features. Support for this proposition comes from an fMRI study by O’Craven, Downing and Kanwisher, (1999). In their study they had a stimuli comprising three elements: a face, a house and direction of motion. The face was transparently overlaid onto the house and either the house or face could move in one of four cardinal directions. In half the blocks subjects viewed a series of stationary houses superimposed on faces that oscillated along one of four axes with a new display presented every 1.4s (Figure 1.7). In the other half of the blocks, the stimulus was identical except the house was moving and the face was stationary.

The subject’s attention was directed to a different attribute in each block by instructing them to monitor the images for consecutive repetitions of either the face, the house or the direction of motion. In order to measure the neural response to each part of the stimlulus, O’Craven et al. (1999) employed a functional localiser in order to define the three region of interest: FFA, PPA and V5/MT, in each subject. They then calculated the average percentage BOLD signal increase relative to baseline (fixation) for each of the six experimental conditions. The six conditions consisted of either the house or face moving and the subject would be asked to attention to either the face, house or direction of motion.

Figure 1.7 shows the stimuli used in O'craven et al. (1999) study. The subject was asked to either attend to the face, house or direction of motion. Either the house or the face would move in one of four directions. The subjects carried out a repetition detection paradigm. The increase in BOLD signal from the three ROIs were then recorded and contrasted to baseline in order to index the amount of processing of each element of the display. Taken from O'Craven et al. 1999.

There were three key results. First, in each region the change in fMRI signal was greater when the subjects attended to the preferred attribute for that cortical region (i.e. the FFA for faces) than when they attended to a different attribute of the same display, for example, the FFA did not show preferential BOLD to a moving house). This was consistent across all three ROI's. A purely spatial model of selective attention cannot account for these results; if space was the unit of selective attention, then all three parts of the stimulus should be processed, and hence result in an increase in BOLD in all three areas. The second key result showed that when subjects attended to motion, there was a greater signal change observed in the FFA when the faces moved (houses were stationary) than when the houses moved (with faces stationary). The same results were seen in the PPA: signal change was greater when the house moved than when the face moved. This modulation of signal was observed even though both faces and houses were present in each stimulus. Finally, signal change was greater in V5/MT even when the subjects attended to only the identification of a house or face, which happened to be moving. In summary these results support the theory of object based processing; when subjects were asked to attend to the face that was moving, both FFA and MT showed and increase in BOLD. This suggests that even though motion was an irrelevant feature, attention implicitly spread across the face and direction of motion. However, no increase was seen in the PPA, which does not support a space based model of attention which would have predicted that all three features would have been processed to an equal level as they shared the same space. Furthermore, these results cannot be explained by a feature based model of attention as otherwise we would have expected to see a sole increase in BOLD signal in the area that was functional specialised in processing the attended feature. Instead O'Craven et al. (1999) argue that even when a task requires that subjects select a given visual attribute, both attributes of the attended object are automatically selected (motion and face or motion and house).

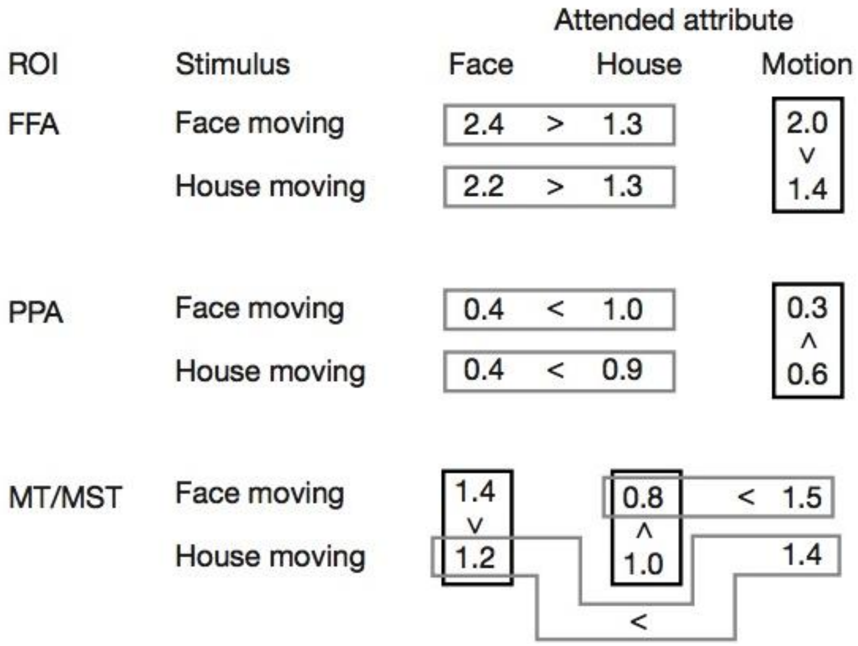


Figure 1.8 shows the results from O'Craven et al. (1999). For each condition the average per cent signal change across subjects is given for each ROIs. The grey boxes show the greater response in each ROI to the attended attribute compared

with the unattended attribute. The black boxes show the greater response to the irrelevant attribute of the attended object compared with the unattended attribute of the unattended object, as predicted only by object-based theories of attention. Taken from O'Craven et al. (1999).

The results displayed in figure 1.8 are compatible with the 'biased competition' model (Desimone and Duncan, 1989) of attention. Although the results show that the irrelevant feature was processed, as indexed by the increase in BOLD in the respective ROI, the percent signal change was smaller when the feature was irrelevant as opposed to relevant to the task. The biased competition model posits that objects trigger neuronal representations that will compete for attentional resources. These competitive interactions have the ability to be biased in preference of one stimulus due to many different neural mechanisms – such as feedback bias. This may be weighted in favour of top down feedback (task relevance) or bottom up influences (a stimuli being more novel than another). Finally the 'biased competition model' posits that feedback biasing is not purely the result of spatial location. Biasing during processing can be due to a stimulus possessing a more relevant feature. Therefore the data from O'Craven et al. may be interpreted as follows: The instruction to attend to one part of the stimuli (such as motion) results in a top down bias signal (Kastner, Pinsk Weerd, Desimone & Ungerleider, 1999) which enhances responses in regions coding that part of the stimuli (i.e. V5/MT for motion). This increased response to the attended part causes an enhancement of the neural response to the other attributes of the same object (i.e. the PPA will show an increased response to the house). This enhancement occurs even when the task does not require the subjects to bind the visual attributes of form and motion. This study complements the object file model which proposes that all features of an object become spontaneously integrated and stored in an object file upon viewing.

Further support for this notion comes from a recent fMRI study by Yi et al. (2008) who found that face selective regions in the FFA exhibited significantly less activation when (task relevant) faces were repeated in (task irrelevant) continuous versus discontinuous trajectories, suggesting that discontinuity caused featurally identical objects to be represented separately. This data indicate that spatiotemporal continuity modulates the neural representations of objects, where a continuous trajectory may lead to the updating of an object file, whereas a discontinuous trajectory may lead to a new object file to be created each time that stimulus is encountered. This supports the location driven model of object files as suggested by Kahneman et al. (1992).

This data supports the observation that when two stimuli are presented in close spatio-temporal succession there is an interaction that is dependent on the relationship between the features of the newly presented object (S1) and the original object (S2). The object file model predicts that that when the newly presented object is a partial repetition of the original object there is a reactivating and updating of the object file formed during the initial representation, with the new feature conjunction information gained from viewing the second presentation of the stimulus. This process carries with it a measurable reaction time cost (termed partial repetition cost), however the neural mechanisms underlying the hypothesized object file retrieval are unknown. In order to identify the neural correlates of the partial repetition cost Keizer, Colzato and Hommel, (2008) carried out an fMRI study to test whether reviewing a particular stimulus reactivates the features of the object it previously accompanies. The features used to address this question were motion, faces and houses, which activate distinguishable regions of the occipito-temporal cortex (O'Craven & Kanwisher, 2000).

These features were also chosen as they have been shown to integrate previously (O’Craven et al. 1999). On each trial, either the face or the house moved in one of two possible directions and participants were instructed to respond as quickly as possible to the direction of the motion in the object that was presented second (S2)

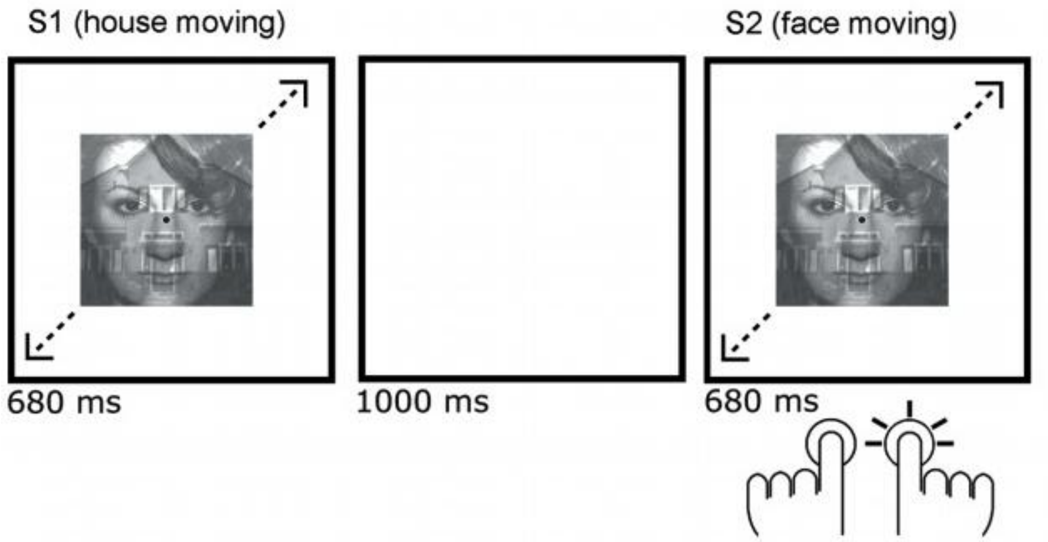


Figure 1.9 shows an example of a trial. S1 consists of a face superimposed on top of a house, however either the face or house can move diagonally in the direction shown by the arrow. Subjects are advised that S1 is irrelevant however they are to passively attend to it. When S2 appears they are instructed to respond to the direction of motion as quickly as possible disregarding the house and the face stimuli. Partial repetition costs are often seen when there is a partial repetition between S1 and S2 e.g. if a house moves top right – bottom left during S1 while the house remains stationary, however during S2 the house moves top right – bottom left during S2 there is a partial repetition cost seen due to the repetition of one feature (direction of motion) and not the other (house or face). This reaction cost is measured against reaction time observed when all features change.

In order to measure the presence of a reactivation effect in the PPA, Keizer et al. (2008) contrasted the conditions in which the direction of motion repeated between S1 and S2 but the object that moved (house or face) alternated (partial repetition trial) against a trial where the motion alternated between S1 and S2 and the object which moved also alternated (all features change trial). If repeating the direction of motion reactivated the representation of the house, it would be expected that there would be an increase in RT and increased activation in the PPA compared to the condition in which all feature changed between S1 and S2. The results confirmed their hypotheses: alternating the object that moved (face/house) but repeating the direction of motion was associated with a RT cost relative to alternating the direction of motion. Furthermore the PPA was more active on these ‘partial repetition’ trials that on ‘change all’ trials. They also carried out a correlation between the RT cost as measured at the individual level and the level of activation in the PPA. There was a significant positive correlation (the higher the RT cost, the higher the BOLD signal in the PPA).

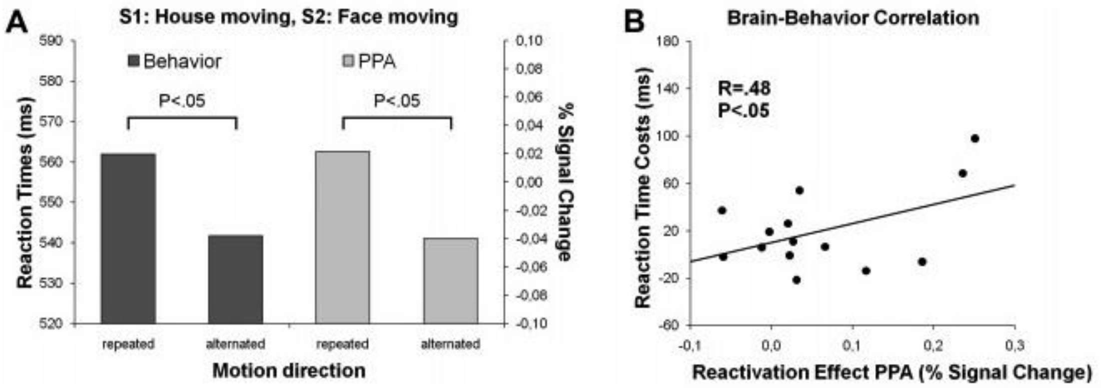


Figure 1.10 shows the results from Keizer et al. (2008). Diagram A. shows the difference in RT during a trial where the motion direction repeated (but object moving (house) alternated) versus trials where the motion direction and the object moving (house) alternated. The right hand side of the graph shows the measurement of BOLD signal in the PPA during those trials where motion direction repeated or motion direction alternated. Diagram B shows the correlation between the RT cost observed at the individual level versus the % signal change observed in the PPA. Taken from Keizer et al. (2008).

However, Keizer et al. (2008) did not reproduce the results in the FFA. Although they did observe a significant partial repetition cost they did not see a significant difference in the percentage signal change in the FFA. The correlation between individual reaction time costs and the percentage BOLD signal change was marginally significant however it was not as robust as the correlation observed in the PPA.

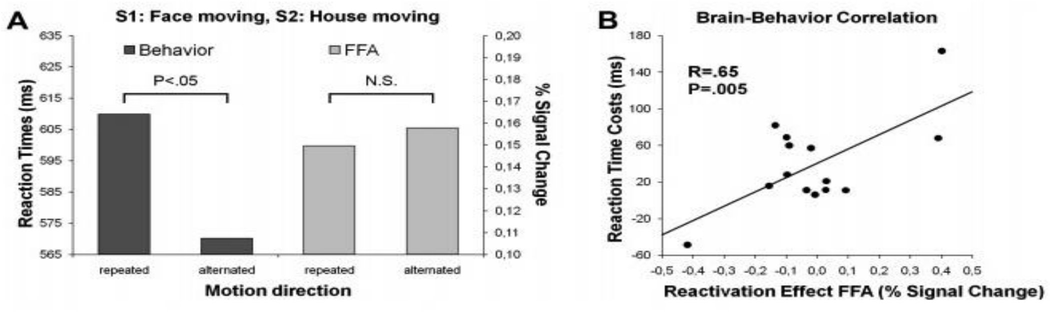


Figure 1.11 the results seen in the PPA were not mirrored in the FFA. Diagram A. shows the RT cost observed when motion direction repeated but the object that moved (face) repeated versus trials where both the motion direction and the object that moved (face) alternated. Although the behavioural result was present and the correlation between BOLD signal and RT cost was both significant and positive.

This experiment provides support for the object file hypothesis and supports the view that a presentation of a stimulus feature that overlaps with a previous object representation leads to reactivation of the feature that it was previously bound with. Keizer et al. (2008) go on to argue that the positive correlation between the observed reactivation of the PPA and partial repetition cost is consistent with the possibility that the neural reactivation caused the corresponding performance costs. However a correlation cannot be used to infer causation therefore I feel this notion may be stretched beyond what the data can offer. The lack of activation in the FFA is not unsurprising if you consider the 'special' role that faces play in perception. There is evidence that stimuli of greater biological significance such as faces, attract more attention and induce more activation (Vuilleumier, 2000; Ro, Friggel & Lavie, 2007). This may have led to an increase in processing of the face stimuli in each trial and hence a larger BOLD signal in each trial, hence leading to a non-significant difference between conditions.

The dissociation between areas of the brain in processing features is useful when looking at the processing conjunctions of features. Although a partial repetition cost has been shown amongst low-level features such as colour and motion there has not been an fMRI study that looks for unique activation within these areas using the above paradigm. Faces and houses are complex stimuli and may lead to potential confounds as observed with face stimuli.

As previously stated, experiment 4 (Chapter 5) aims to expand the functional neuroimaging literature exploring the neural correlates of object files. However, in order to avoid the confounding effects of using already complex stimuli, low-level features such as motion and colour are employed. Further to this, a novel adaptation is incorporated in order to answer the question of whether task irrelevant feature changes get processed via a separate cortical route to that of task relevant feature changes.

1.5 Feature binding and the aim of this thesis

At the outset of this Introduction, feature binding was introduced as a problem that the brain has to solve during the process of perception. The neural networks engaged during both explicit feature binding and implicit feature binding, were briefly introduced, as this is what will be explored in fMRI Experiments 1 and 4, respectively. Following this, other sections have outlined competing models of feature binding and provided a review of the relevant feature binding literature. Below the experiments comprising the bulk of this thesis are outlined.

The first experimental chapter is an event related fMRI that employs a novel paradigm in order to compare the neural correlates of spatial detection, temporal order judgement and an explicit feature conjunction judgement. Previously, studies have either compared a feature conjunction task to either a spatial task or a temporal task, or a temporal task to a spatial task and in doing so have often not controlled for low-level stimuli differences (Shafritz et al. 2002). However, no study, to the best of my knowledge, has compared all three tasks whilst controlling for difficulty and low-level stimulus differences. By controlling these factors, experiment 1 aimed to tease out areas of the brain that may be uniquely engaged during feature binding by comparing all three tasks. As previously mentioned, there is evidence that unique areas engaged in feature binding may lie in the parietal cortex, on the contrary recent studies have suggested that coding for conjunctions can be detected at lower level that are relevant to the stimulus being bound. For this reason both a whole brain analysis and a region of interest analysis focussing on V1, V4 and MT will be implemented in order to address this question.

Experiment 2a and 2b (Chapter 3) tests the boundaries of the object file model previously discussed. By using two non-spatial features (colour and motion), I examine the composite elements of an object file, and also the conditions that lead to a partial repetition cost. Using semantically linked words, I test whether partial repetition costs can be caused by more than just veridical features, do object files also carry or link to long term memory structures allowing for semantic cross-over for physically dissimilar stimuli? The literature surrounding integration of semantic information has not been introduced in this chapter, in order to avoid repetition; however this is discussed in the introduction of experiment 2b. Further to this, I separate the partial repetition cost caused by non-relevant feature changes and those caused by irrelevant feature changes. Alongside the important theoretical implications of the role of irrelevant features in feature binding this also allows us to control for motor switch costs across conditions which was not controlled in the earlier studies (Kahneman et al. 1998) and were controlled by introducing a further motor component by later studies (Hommel, 2004).

Following the identification of flaws in experiment 2a, experiment 3 (Chapter 4), employs two integral modifications in order to increase the robustness of the results: firstly, shape and location were introduced as features which were controlled and manipulated, secondly, the area over which the stimuli was presented was decreased. This made the stimulus more object like and therefore led to a more robust partial repetition cost driven by both an irrelevant and relevant feature change. This modification, I ask the question of whether different features (shape, location, colour or motion) lead to equal repetition costs, and therefore play an equal role in the formation and reactivation of object files. In order to answer this question, subjects completed four separate sessions in which the feature that was relevant and irrelevant to the response changed between shape, colour, motion or location.

Chapter 5 looks to establish the whether there is a neural network engaged the formation or reactivation of an object file. The functional neuro-imaging literature is severely limited in this area (Keizer et al. 2008) and previous studies have predefined regions of interest prior to analysis, therefore in order to allow a thorough investigation of the areas of the brain engaged during the formation or reactivation of an object file, a whole brain analysis was carried out. During the functional neuroimaging, one feature block (motion) is completed as opposed to the four completed in chapter 4, meaning motion is the feature which is task relevant and the subjects must respond to; location, shape and colour are task irrelevant. This allows us to look at feature specific processing areas (MT) alongside a whole brain analysis in order to identify the neural correlates of a partial repetition cost.

Finally the, first experiment to employ cTBS alongside the reviewing paradigm, experiment 5 (Chapter 6) looks to establish the causality of the areas that showed a functional increase in BOLD in experiment 4, during in the updating or reactivating of an object file. The aim of this experiment was to establish the causality of these areas within the formation and updating of object files. In order to do that cTBS is applied offline prior to the subjects carrying out the task in three separate cortical areas, namely the right LOC, left PCG and left SFG. The RT modulation is then contrasted to a sham condition, in which no cTBS is applied.

These experimental chapters are complemented by a general discussion (Chapter 7) in which the findings from the five experiments are summarised, and integrated, and where key outstanding questions are considered in the context of the diverse literature presented in the introduction.

Chapter 2 - Experiment 1

Using fMRI to distinguish the neural networks engaged during visual feature binding in contrast to temporal order and spatial location detection

2.1 Introduction

The concept of functional specialisation is one of the key principles of visual processing. Originating from lesion studies carried out in the macaque monkey (Cragg 1969; Zeki et al. 1991), there is now a large body of evidence demonstrating functional specialisation in the human visual cortex (Jbabdi et al. 2012; Kanwisher, 2010). The modularity of visual processing is evident from the earliest stages of cortical visual processing. Colour and motion are processed in two functionally and anatomically distinct cortical areas, V4 and V5/MT respectively (Vaina, 1994). Although not exclusively specialised, V4 plays a key role in processing colour (Zeki, 1973, 1974b, 1977), that is in contrast to the processing of motion, which is shown to take place in visual area V5/MT (Bartels & Zeki, 2000; Shipp & Zeki, 1995).

As information progresses, two streams of processing emerge; namely the ventral and dorsal streams. These pathways are not only distinguished on functional grounds but also because they are subserved by distinct anatomical substrates in the brain (Ungerleider & Haxby, 1994). Much evidence shows that areas in the ventral (‘what’) pathway, extending from the striate cortex to the infero-temporal cortex, play a major role in object recognition (Haxby et al. 1991; Mishkin, Ungerleider & Macko, 1983). In contrast, spatial processing and sensorimotor transformations, necessary for visually guided action, are believed to be coordinated by the dorsal (‘where’) pathway, which originates in V1 and extends forward to the parietal cortex (Goodale & Milner, 1992).

Vision is an active process in the sense that the brain is constantly creating the visual environment in which we interact. In order for this to be carried out efficiently and accurately there is a need for both parallel and simultaneous processing of information. The seamless efficiency with which the brain computes and integrates information may lead to the conclusion that perception is effortless and integration of separately processed information is integrated with little or no cognitive effort. However, swhen this 'binding' mechanism breaks down or is perturbed we can observe the extent of the division of labour during visual processing, which in turn, requires a high level of integration when reconstructing a visual percept.

As discussed previously in Chapter 1, Balint's syndrome is a rare condition that allows a glimpse into a visual world where integration has failed (Rafal, 2000). The mismatch of correctly perceived features, across space and between objects, has been termed an 'illusory conjunction' (Treisman, 1982). The report of an illusory conjunction is thought to reflect a failure of the feature binding mechanism, as the result is the incorrect report of a pairing of correctly perceived features. Illusory conjunctions and the feature binding difficulties observed in patients with visuo-spatial deficits have led to the conclusion that there is a high level of integration being performed within the visual processing stream. These observations lend support to a model developed by Treisman and Gelade (1980) called the 'feature integration theory' (FIT). This model proposes the process by which visual integration might be achieved. The main assertion of the FIT is that features can only become bound together following the allocation of spatial attention. Spatial attention is proposed to feature 'glue', which is to say that when spatial information is not available, or a patient has lost the ability to process space, features are prevented from becoming bound and therefore objects are seen incorrectly or not at all.

Although many studies have shown that spatial information plays a pivotal role in the processing of the visual scene (Robertson, 2003; Holcombe, 2009), the exact nature of this role is still highly debated (Shafritz, Gore & Marois, 2002). Since the FIT was proposed in 1980, the integrative mechanism has proved to be more complex than the FIT suggests, with studies showing successful feature integration without attention (Wojciulik & Kanwisher, 1998) and even without awareness (Melcher, Papathomas, Vidnyánszky, 2005).

As previously explored in Chapter 1, much evidence for feature binding and the possible mechanisms of action comes from patient studies. A key patient that has been observed extensively during feature binding tasks is Patient R.M. R.M was diagnosed with Balint's syndrome following two strokes that led to the obliteration of both of his parietal cortices. One of R.M.'s main symptoms is the loss of spatial information, which led to high levels of illusory conjunctions. These illusory conjunctions were observed when the subject was presented with two coloured letters side by side and asked to report the form and colour pairing in-front of him. The results showed that patient R.M often paired the wrong letter with the wrong colour, thus suggesting that the loss of spatial information was a key reason why the patient could not accurately bind features together. To determine whether R.M. would exhibit feature binding deficits when the stimulus was presented across time instead of space, that is in the same spatial location but at different times, the patient completed the same task again but with the stimulus presented sequentially. The results showed a significant reduction in illusory conjunctions when the letters were presented sequentially in the same location as opposed to concurrently across different locations; this prompted the interpretation. This case study prompted the conclusion that the feature binding deficits exhibited by patient R.M. resulted not from a breakdown in the neural apparatus used to integrate features *per se*, but from impairment in the apparatus needed to represent the space that the object is bound within (Cinel & Humpreys, 2006).

On this basis, the aim of this study was to distinguish the three potentially separate processes apart of spatial processing, temporal processing, and explicit feature binding. To achieve this I developed a paradigm in which subjects were either cued to make a feature conjunction judgement (report the combination of motion and colour), a spatial discrimination judgement (report whether the patch of moving dots is more to the left or right of a central fixation point), or a temporal order judgement (report whether the patch of dots appeared before or after the fixation cross changed colour). During the feature conjunction task, subjects needed only attend to the conjunction of features (the combination of colour and direction of motion) and were told that the spatial position and temporal onset of the visual stimuli was irrelevant. Similarly, when subjects complete the spatial discrimination task, they were instructed to attend only to whether the patches were more to the right or left of fixation, with the feature conjunction (colour and motion pairing) and the temporal onset of the dots considered irrelevant.

Finally, when attending to a temporal onset (did the dots appear before or after an event?) the feature conjunction and the spatial position of the dots were task irrelevant. Contrasting activation states associated with these judgements while holding the stimuli constant allowed the direct contrast of neural activity when either explicitly attending to space, time, or a conjunction of object features.

‘Where?’ – spatial discrimination task

In the current paradigm, the feature conjunction task was contrasted with a spatial discrimination task in which subjects judged whether the green and red patches of dots were more to the left or right of fixation. The patches of dots were independent of one another; therefore the position of one patch of dots could not be predicted from the position of the other patch. This type of spatial processing is often referred to as coordinate spatial processing. Attending to the coordinate spatial relations of an object is distinct from attending to the identity of objects (Amorapanth, Widick and Chatterjee, 2010). Coordinate representations, and hence spatial discrimination, are critical to guide movements such as reaching and navigation, which may lead to the assumption that the dorsal pathway may be engaged during such tasks. There is much research to support that the brain areas engaged during a spatial discrimination task are lateralised to the right side of the brain (e.g. Kosslyn, 1987).

Since then, two fMRI studies have shown that an increase in the right parietal cortex correlated with coordinate relation processing (Baciu et al. 1999; Trojan et al. 2002). Furthermore, the dorsal pathway is hypothesised to play a major role in spatial localisation of stimuli, and be a key component in the action pathway. Specifically, it is thought the cortical regions within the dorsal pathway compute the spatial relations between objects in the environment to allow for effective interaction. Therefore, as per the dorsal pathway shown in Fig 2.1, it was hypothesised that the spatial discrimination judgement would lead to a significant increase in BOLD along the areas in the dorsal pathway such as V1, right intra-parietal sulcus and right superior parietal lobule.

‘When?’- temporal discrimination task

Although temporal information and explicit temporal order judgements are crucial to many aspects of human performance (Rao, Mayer & Harrington, 2009), temporal attention remains a relatively impoverished area of research, in contrast to spatial attention.

Processing temporal information can occur on many scales. Battelli et al. (2007) asserts that the most complex level of temporal processing is at the intermediate scale (between 1 and several seconds), yet this is also the least understood (Burr & Marrone, 2006). As previously explored in Chapter 1, a temporal analogue of the spatial orienting of attention task (Posner 1980) was developed in order to identify the cortical network engaged during temporal attention (Coull & Nobre, 1998). This enabled the dissociation of spatial and temporal attention by solely manipulating the top down allocation of attention to either a point in space or a point in time, yet keeping the task identical and equating low-level stimulus characteristics. The visual display consisted of a central cue and two peripheral boxes inside which the target appeared. The subjects' task was to explicitly detect the peripheral target stimuli as rapidly and as accurately as possible. The task manipulated subjects' expectations of *where* or *when* target stimuli would appear within the experimental display. Using fMRI and PET, Coull and Nobre (1998) observed a striking hemispheric lateralisation for attention to spatial location versus temporal interval with preferential activation for the right and left parietal areas, respectively.

However, due to possible task confounds and different methodology, evidence in support of hemispheric lateralisation has not been consistent. During the aforementioned study of Coull and Nobre (1998), the spatial condition elicited a significantly slower RT in contrast to the temporal attention task, indicating a higher level of task difficulty, which has in turn been shown to be associated with changes in activity in the right parietal cortex (Drager et al. 2004).

Further evidence of a lateralised domain specific attentional network comes from a recent fMRI study in which BOLD selectively increased in the left temporo-parietal junction (TPJ) during a temporal order judgement (TOJ) in contrast to a feature judgement (Davis et al. 2009). Participants were asked to either make a shape judgement or a TOJ of rapidly presented, spatially separated stimuli. Participants were presented with a sequence of two rectangles, which contained two grey lines of different widths. Prior to each trial, participants were cued by a coloured central fixation point to either attend to the width of the grey line or the temporal onset of the rectangles. Depending on the conditions, they were then required to identify which grey line was wider or which rectangle appeared first. This paradigm allowed researchers to compare the neural response to physically identical stimuli, and observe differences in BOLD specific to each task, namely the temporal task and the feature task. In line with the hemispheric lateralisation of temporal attention reported by Coull and Nobre (1998), Davis et al. (2009) reported the selective involvement of the left TPJ, the left supra-marginal gyrus (SMG) and the left IPS during the TOJ whereas the contrast of shape>temporal order judgement led to no significantly activated voxels. Although the physical stimuli were matched between tasks, the shape judgement yielded a significantly lower accuracy compared with the temporal order judgement; therefore leaving open the possibility that the observed task-specific activations were driven by systematic variation in task difficulty rather than the engagement of categorically distinct perceptual or attentional processes. In addition, compared with Coull et al. (1998), different statistical contrasts were used to identify the different cortical areas active during a temporal task. While Coull et al.(1998) compared a temporal and a spatial task independently to a baseline (BL) and then contrasted the two outcomes with each other, Davis et al. (2009) directly compared temporal attention to feature based attention. Due to the subtractive nature of fMRI statistics, this inconsistent comparative approach could lead to results that are not necessarily reflective of anything but the contrast that is calculated during that specific analysis, and therefore not comparable across the literature.

Further conflicting results are born out of studies of neural interference. Patients with right (Baylis et al. 2002; Rorden et al. 1997; Robertson et al. 1998; Sinnett et al. 2007; Snyder and Chaterjee, 2004) or left (Baylis et al. 2002) hemisphere injuries can exhibit biased performance on a TOJ. However, recently Woo, Kim and Lee,, (2009) reported that disrupting the right but *not* the left parietal cortex, using transcranial magnetic stimulation (TMS), led to biased TOJ performance. Bringing together results primarily from TMS studies, Battelli et al. (2007) recently proposed that temporal information is processing along a ‘when pathway’ that co-exists alongside the dorsal and ventral streams (see Fig 2.1).

‘What?’ – feature conjunction task

Although feature binding has been correlated with activity in the parietal cortex (Friedman-Hill et al. 1995; Karatekin et al. 1999; Ashbridge et al. 1997) this may be reflective of the spatial context in which the information is being bound. Recently, evidence of colour-motion binding, as early as V1, has been observed (Seymour et al. 2009). As noted earlier, colour and motion are processed primarily in V4 and V5/MT respectively. The selectivity of these areas has been confirmed causally in patients with lesions in the area of V4 showing impaired colour perception but spared motion perception, whereas the opposite is true for lesions to the V5/MT complex (Damasio, 1985; Vaina, 1994).

In order to establish whether the lower visual areas do contain feature conjunction information, Seymour, Clifford, Logothetis and Bartels (2009) used fMRI and MVPA to explore whether lower visual areas such as V4 and V5/MT contain information regarding the conjunction of motion and colour, or contain purely information on either motion or colour. The stimuli consisted of two transparent motion stimuli that each contained the same two colours and two motion directions but differed exclusively in their unique pairings, (i.e red clockwise and/or green anticlockwise). Using pattern classifiers, Seymour et al. (2009) found that information about the colour and motion pairing was present to varying extents across the visual cortex. They found evidence for conjunction coding as early as V1 and across the entire visual cortex. However, no colour information was present in V5/MT. A further study by Seymour, Clifford, Logothetis and Bartels (2010) was carried out using the same methodology. However this time they looked at the conjunction of colour and orientation. Again fMRI and pattern classifiers were applied to examine whether BOLD signals in human visual cortex could correctly discriminate stimuli that differed only by their specific pairing of colour and orientation. Their results showed that conjunctions of colour and orientation could be decoded from patterns of activation as early as V1. However they also found that the most informative voxels about the conjunction of colour and orientation did not overlap with voxels most informative about colour or orientation alone. This suggests that separate functional units may be tuned to specific combinations of colour and orientation (Seymour et al. 2010) – a neural 'signature' of feature binding.

In order to fully examine the areas of the brain that were engaged in an explicit feature conjunction task, experiment 1 of this thesis included an ROI analysis on areas V1, V4 and V5/MT. V4 and V5/MT were specifically examined due to their specialised role in processing colour and motion respectively. If feature binding was to take place in the lower visual cortex and in areas specific to processing those features then a task that requires attention to feature conjunctions should elicit an elevated BOLD signal compared with spatial discrimination and temporal order judgements.

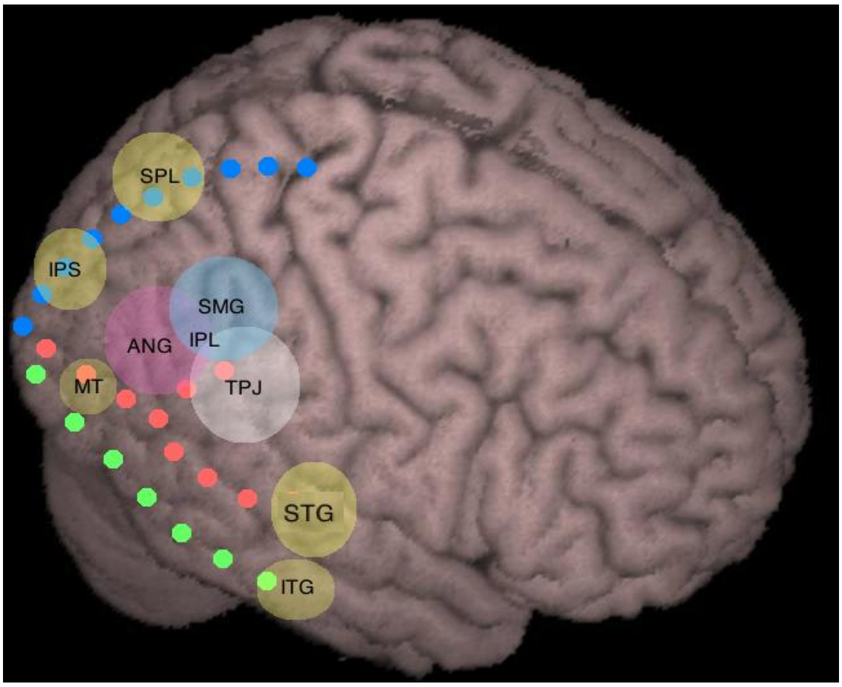


Figure 2.1. The three proposed pathways of visual processing of temporal, spatial or object based processing. The dorsal pathway is represented using blue dots, the temporal pathwa using red dots and the object-based pathway using green dots. The newly proposed temporal pathway (Battelli et al, 2007) extends from V1 into a larger network with the key anatomical locus being the TPJ within the IPL. However, the pathway is thought to include a wider network of the right ANG, the SMG and the STG. MT = medial temporal; IPS = intra-parietal sulcus; SPL = superior parietal lobe; ANG = angular gyrus; SMG = supramarginal gyrus; IPL =

inferior parietal lobe; TPJ = temporo-parietal junction; STG = superior temporal gyrus; ITG =inferior temporal gyrus.

Dual tasks

To permit manipulation of attention without altering the physical properties of stimuli, all information for all possible tasks had to be present in each trial. Therefore, it was important to ensure that top-down selective attention was engaged. The load theory of attention (Lavie, 1995, 2005) suggests that the extent to which irrelevant stimuli are processed depends on the level of perceptual load required by the prevailing task. To ensure that selective attention was under sufficient load, participants completed some trials in which they attended to two aspects of the stimuli. For example, the spatial (S), temporal (T) and conjunction (C) tasks were combined into three dual task conditions: ST, TC and SC. Statistically contrasting TC trials to SC trials (TC-SC) would then allow us to observe areas that are specifically engaged during temporal order judgments that may not be observable under the low perceptual load of the single temporal trials. An alternative approach would have been to increase the difficulty of the single task conditions; however, most subjects were at the highest difficulty setting in order to calibrate accuracy to 70%. Therefore increasing attentional load was considered the most appropriate method for increasing task demands.

In summary, the aim of this experiment was to establish whether there is a dedicated neural circuit for explicit, task-relevant feature binding over and above processing of space and time. More specifically, are distinct brain areas selectively recruited during the reporting of an explicit conjunction of motion and colour in contrast to a spatial discrimination task or a temporal order judgement? To examine this all low-level task differences and task difficulty were held constant or matched as closely as possible across the three tasks.

2.2 Materials and Methods

2.2.1 Participants

The experiment consisted of three parts: behavioural thresholding, retinotopic mapping and fMRI scanning while completing the task. Seventeen healthy right-handed participants were recruited for all three parts of the experiment (Mean age = 21 SD = 1.5 years, 11 females). All participants had normal or corrected-to-normal visual acuity and had normal colour vision. Each participant also completed a safety screening prior to the experiment to ensure they were eligible to enter the MRI scanner. They gave their written informed consent to the experimental procedure, which was approved by the research ethics committee at the School of Psychology, Cardiff University.

2.2.2 Apparatus

The initial behavioural experimental sessions were conducted in a darkened laboratory. Visual stimuli were presented at a mid-sagittal viewing distance of 50cm, on a 21–inch CRT monitor (60Hz vertical refresh rate; 1024x768 resolution; black background). Throughout the experiment the participant's head was fixed within a chin rest. Although gaze was not monitored with eye tracking, participants were asked to focus on the fixation cross at all times.

2.2.3 Paradigm

Every forth trial would begin with a cue that indicated whether subjects would need to complete a temporal, spatial or feature conjunction judgement during the upcoming trial (see Figure 2.2). During dual task trials the cue would indicate which two of the aforementioned tasks the participant would need to complete (Figure 2.5).

INSERT FIG 2.2 HERE separate page .

Figure 2.2 A. An example trial from the 'what', 'where' and 'when' conditions. The cue indicates the task that the subject will complete for the next four trials until a new cue appears. The red and green boxes represent patches of moving dots; presented as red or green squares for clarity. B. The temporal structure of a trial. This example trial is for a single task. The cue is shown initially and is valid for four trials; the following 3 trials are preceded by a cue.

The cue presented at the beginning of trial 1 was valid for 4 trials, indicating that the subject would perform the same task 4 times before the presentation of a different cue. The cue always switched to ensure that participants never performed more than 4 repetitions of each condition during a scanning block. As shown in Figure 2.2, the cue was immediately followed by a centrally presented white fixation cross. At 1500ms two square patches of moving dots would appear. The coherence of the dots was dependent on the individual threshold-level; in each patch there was a density of 50 dots per patch; each patch was 50mm x 50mm and the coherent dots moved at 0.6 degrees per second. One patch of dots would appear above the fixation cross and the other below. The fixation cross could change from white to yellow at any time, in sync with the screen refresh rate of 16.7ms. Each patch could appear shifted to the left or the right, relative to the centre of the fixation cross. The amount in which the patch was shifted was set in accordance with the individual psychophysical thresholds; this also established the ease of the task. The temporal sequence of a single task trial is summarised below in Figure 2.3.

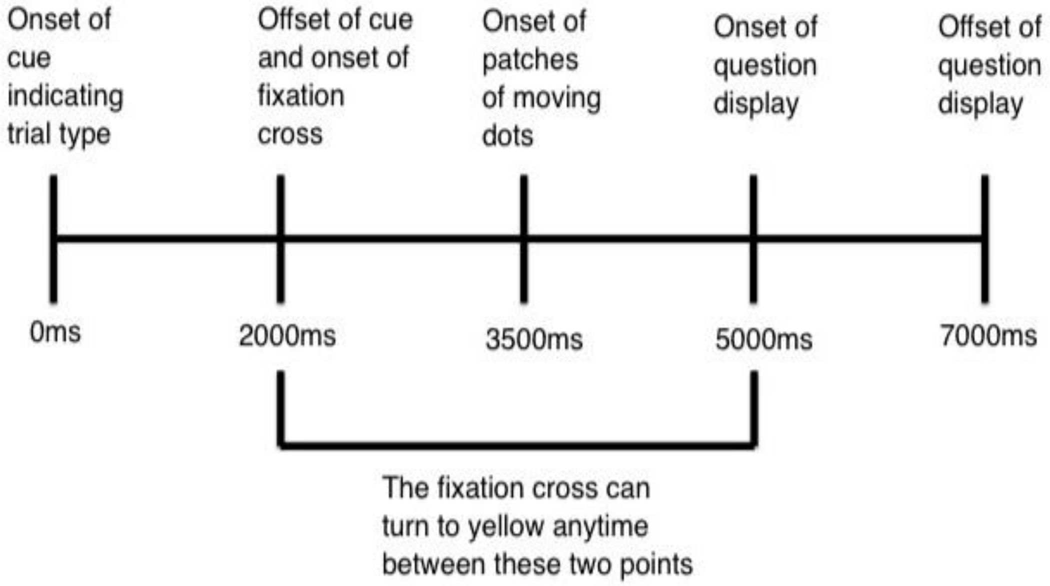


Figure 2.3 The timeline of a single task trial. The dual task trial would be identical apart from the added question at the end; extending the total time of a trial to 9000ms.

The single task trials could begin with the cue of either: "What?" "Where?" or "When?". These cues indicated a feature conjunction task, a spatial discrimination task or a temporal order task respectively. The colour of the stimulus that the participant is asked to attend to is counterbalanced across the block. The accompanying questions to these cues were as follows:

- Where? - Red: Left or Right? – This asked the participant whether the red patch of dots were more to the left or right of the central fixation cross.
- When? - Green: Before or After? – This asked the participant whether the green patch of dots appeared before or after the central fixation-cross changed from white to yellow.
- What? - Red: Up or Down? – This asked the participant whether the red patch of dots consisted of dots moving mostly up or mostly down.

The participant responded with either a left or a right button press using their index or middle finger, respectively, in response to the question displayed on the screen. If the answer on the left was correct, the index finger was used to respond with a left button press and if the correct answer was on the right then the middle finger was used to press the right button. Participants had 2000ms to respond. The first response was the only response that was recorded. Single task trials would last for 7s (Figure2.2), whereas dual task trials would last for 9s (Fig 2.4). Due to necessary jittering between trials, each participant had an unpredictable break of 2-8s in length. This was calculated in increments of 500ms and occurred after each trial. Each experimental block consisted of 48 trials; including 8 per condition, and a total of 6 experimental blocks were completed per participant. Each experimental run lasted for approximately 9 minutes.

INSERT DIAGRAM OF DUAL TRIALS HERE 2.4

Similarly to the single task conditions, the dual task trials could consist of either the cue: “What & Where?” “Where & When?” or “When & What?” and the accompanying questions at the end of the trial were as follows. Question 1 (Q1) and question 2 (Q2) were presented separately for 2000ms each:

What & where?	Q1: Green: Up or Down?	Q2: Green: Left or Right?
Where & when?	Q1: Red: Left or Right?	Q2: Red: Before or After?
When & what?	Q1: Green: Before or After?	Q2: Green: Up or Down?

Each participant completed a brief colour calibration to ensure the red and green dots were of equal luminance. This was carried out using a MATLAB script that changed the luminosity of the dots on screen when the mouse was moved left or -right on the desk in-front of the subject. When the subject felt the luminosity was matched between the red and green dots they pressed the left mouse button and the two colour codes were recorded. This was important to ensure that no particular set of dots attracted more attention than the other.

Thresholding of behavioural task

Thresholding consisted of a 90-minute session in which participants’ accuracy threshold was set to 70%. Using a method of constant stimuli, this was completed offline, in a behavioural testing lab. In order to assess the subjects’ threshold, participants undertook 100 trials in each condition (T, S, C, ST, SC, and CT). Rest periods were offered at the completion of each block. In order to threshold the temporal task, the time between the change of the colour of the fixation cross and the onset of the dots was either lengthened or shortened making a temporal order judgement easier or more difficult. The spatial task varied the degree to which the squares of moving dots were shifted over the centre of fixation (see Figure 2.5) below. The feature conjunction task, in which subjects had to decide whether the red or green dots were moving up or down, were a mixture of coherently moving dots, either moving up or down at 0.6 degrees per second or replotted at 63hz in order to give the impression of incoherent noise. The degree of coherent dots with incoherent dots varied during the thresholding session between 100% coherence where all dots moved in one direction to 0% coherence where all the dots appeared to move incoherently.

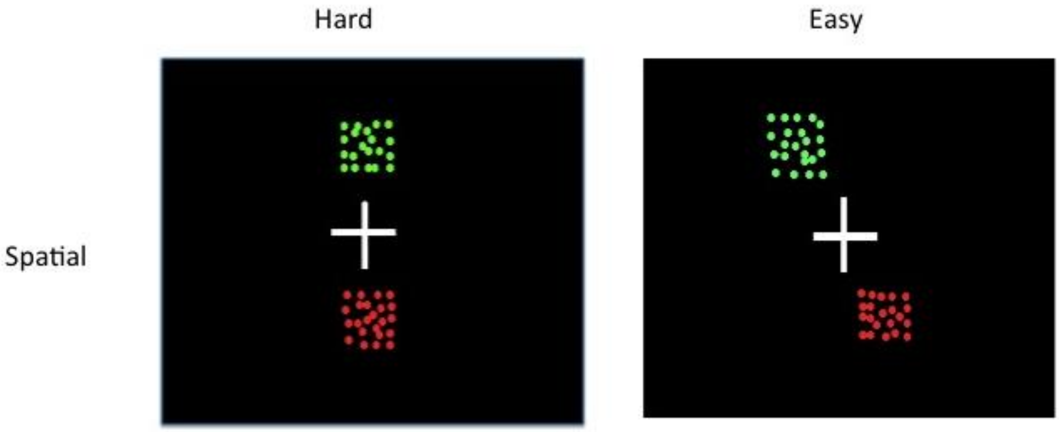


Figure 2.5 shows examples of ‘hard’ and an ‘easy’ spatial trials, respectively. The more central the dots were positioned, the harder the subject found the judgement of left or right. However in an easy trial this was more obvious.

Once all data had been collected we then calculated the ideal stimulus parameters that would produce 70% accuracy across all conditions. The calculated threshold was then set for that participant and would dictate the parameters of the stimulus displayed in the MR scanner during the participant’s scanning session.

2.2.4 fMRI Data Acquisition and Statistical Analysis

All data were acquired using a GE Signa HDx 3T scanner with an 8-channel head RF receive coil. T2*- weighted gradient echo fMRI data were acquired using an echo-planar imaging (EPI) pulse sequence with the following parameters; 53 interleaved oblique-axial slices (orientated along the participants' AC-PC lines) covering the whole brain, TR =3000ms, TE= 35ms, flip angle = 90 degrees, acquisition matrix= 64x64, slice thickness of 3.4mm, spacing between slice =3.4mm, parallel imaging acceleration (ASSET) factor 2. Each scanning sequence was comprised of 152 volumes and lasted for approximately 9 minutes.

Participants completed 6 experimental runs. Each run consisted of 48 trials; 8 per condition.

Anatomical scans were acquired using a T1-weighted fast, spoiled gradient recalled sequence (FSPGR) with the following parameters; 1mm isotropic resolution, acquisition matrix 256x256x176, TR/TE=7.9/3.0 ms, TI=450ms, flip angle=20deg.

Field-maps were collected at the end of each scanning session. The field-map acquisition consisted of 2 SPGR scans with two different echo times of 7ms and 9ms. Field maps were collected because EPI images often exhibit substantial signal dropout and spatial distortion in regions where the magnetic field is inhomogeneous (Bandettini et al. 1995; Hutton et al. 2002). As we cannot recover lost signal, the field maps attempt to remove any distortion from the images. Field maps help make the shape of each individual's fMRI data more similar to their anatomical scan – which improves the quality of the normalisation leading to improved group level statistics.

Stage 1: fMRI data analysis

The fMRI data were analysed using the FMRIB software library (FSL; www.fmrib.ox.ac.uk/fsl). Preprocessing parameters were as follows: motion correction using MCFLIRT (Jenkinson, Bannister, Brady & Smith, 2002); non-brain removal with BET (Smith, 2002). The fMRI data were then registered to the participant's structural scan. All functional volumes were then smoothed with a 55 mm full-width half-maximum (FWHM) isotropic Gaussian kernel to compensate for residual between-subject variations after spatial normalization. The resulting time series across each voxel were then high pass filter cut-off at 1/128Hz. Intra-subject analysis

Statistical maps were generated using a fixed effects model. At the subject level, 6 event types were identified according to the 6 conditions (S, T, C, ST CT and CS), which were separately modelled as either single task events that lasted 5 seconds or dual task events that lasted 7 seconds. Both correct and incorrect responses were included in the analysis. Data was analysed by modelling the evoked hemodynamic response function (HRF) and its hemodynamic temporal derivatives (HRT) in the context of fixed effects general linear model. Contrasts of parameter estimates were then calculated to produce statistical maps for each contrast of interest. Each single task was contrasted with every other single task (S, T & C) and each dual task was contrasted with every other dual task (ST, SC & TC) to produce statistical maps. The single task conditions were not contrasted to the dual task conditions as the analysis of the behavioural data showed that they were not equal in task difficulty. Following the creation of the statistical maps, the fMRI data was then registered to the participant's structural scan.

Group level analysis

The statistical maps then generated at the subject level were then entered into a group level mixed effects model. Voxel based thresholding was then applied to the resulting statistical maps (Z=2.3), and cluster-based thresholding was used to correct for multiple comparisons, with a (corrected) cluster significance threshold of P=<0.05.

Stage 2. Retinotopic mapping and ROI Analysis of V1, V4, V5/MT

Retinotopic mapping data were acquired using a gradient-echo EPI sequence with the following parameters; TR=3.0s, TE=35ms, Flip angle=90°, 128x128 acquisition matrix, 256mmx256mm FOV, 37 2mm thick slices parallel to the calcarine sulcus, 100 volumes, spatial smoothing using a Gaussian kernel of full width half maximum (FWHM) 0.5mm. The stimuli consisted of 70 - degree wedges, rotating at 1 rpm, containing dots that moved and changed in a 3D flow pattern. In each session, two clockwise and two anti-clockwise runs were performed in a counterbalanced manner. Analysis of retinotopic data was performed using in-house software (developed by Krish Singh) that computed phase angle estimates with correction for hemodynamic lag for each voxels and estimated the strength of retinotopy, using the power of the variance in the time series at 1 rpm frequency. The phase angles were plotted as a coloured map on the flattened occipital cortex using mri3dX software, this is downloadable at http://www.cubric.cf.ac.uk/Documentation/mri3dX. Once the functional data was loaded onto the flatmaps three ROIs were defined: V1, V4 and V5/MT.

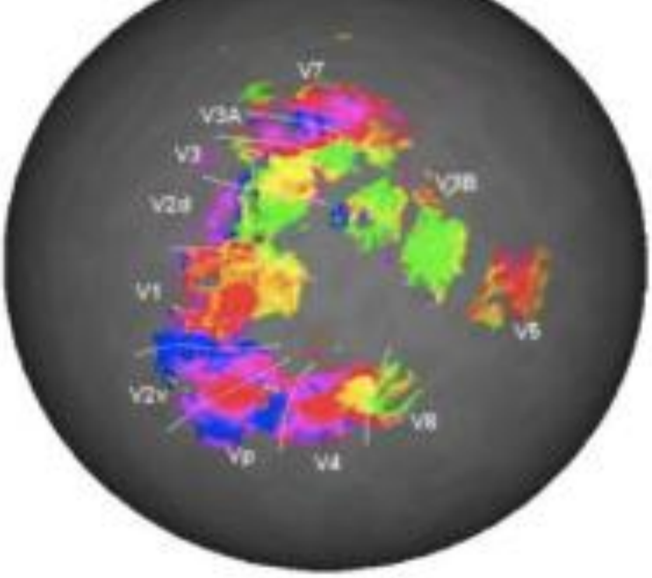


Fig 2.6 V1, V4 and V5/MT were segregated and saved as a ROI mask. This was then applied to the data in order to get a percentage of BOLD signal change in the lower visual areas. Taken from Kurniawan, 2012.

To investigate whether the feature conjunction task led to a significant increase of BOLD above a spatial judgement or a temporal order judgement, an ROI analysis was carried out for each participant. Using retinotopic-mapping data V1, V4 and V5/MT were identified. A mask of each area was then created and entered into Feat-query with the participant's data from the fMRI scanning session. Within each individual's ROI the percentage signal change was calculated for each single task contrast versus every other single contrast, (S>T, T>S, C>S, S>C, T>C, C>T). The percent signal changes were then averaged across participants. A t-test was then carried out to see if the BOLD signal significantly varied from zero during each condition in contrast to every other condition.

2.3 Results

Behavioural results during fMRI scanning

The accuracy was measured for each condition in order to make sure that the difficulty level had remained consistent throughout the scanning sessions. Each subject was calibrated to achieve 70% accuracy during scanning. This was based on the thresholding session carried out individual prior to the scanning session, as previously described in the Methods. Although some practice effects were expected, these were predicted to be consistent across all conditions. The percentage of correct responses during the scanner session for the spatial (S), temporal (T) and feature conjunction (C) task was 83%, 80.9% and 84.8%, respectively. Overall accuracy in the dual task conditions (M=77.86, SE=0.15) significantly lower than in the single task conditions (M=82.97, SE =1.12), t(3)=4.44, p=<0.02). However, a one-way ANOVA revealed no significant differences between task types (S, T, C) within the single task conditions F (7, 16=1.124, p=0.345). Within the dual task conditions, participants performed at 78.2%, 77.7% and 77.6%, respectively, for the spatial/temporal (ST), temporal/feature conjunction (TC) and spatial/feature conjunction (SC) conditions; as with the single task conditions, these did not differ significantly from each other, F (7,16)=0.77, P=0.749.

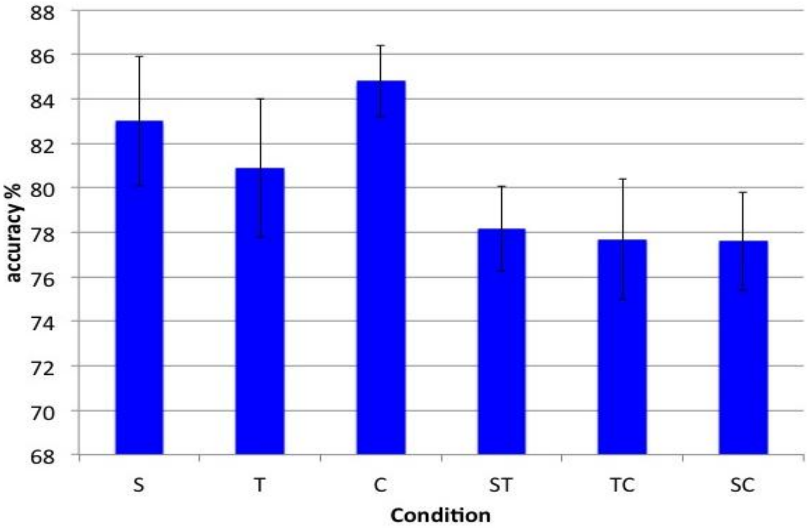


Figure 2.7. Behavioural results, including mean accuracy of each condition across all 17 participants. The mean accuracy is shown as a percentage. The error bars represent the standard error in each condition. S = spatial detection task; T = temporal task; C = feature conjunction; ST = spatial-temporal tasks; TC = temporal-feature conjunction tasks; SC = spatial-feature conjunction tasks. Error bars = SEM.

2.4 Imaging results – whole brain analysis

In order to distinguish the BOLD response associated with the feature conjunction task over and above that of a spatial or/and a temporal task, a whole brain analysis was carried out for all single tasks versus all other single tasks (S>T, T>S, C>S, S>C, T>C, C>T). The three contrasts that led to significant levels of BOLD ($P<0.05$) are presented below. T>S, C>T and C>S did not lead to any significant activations across the brain. The clusters labelled below represent the areas over which the activation was observed. Table 2.1 details where the peak Z-score was observed and therefore may not reflect the areas labelled in figure 2.8 below.

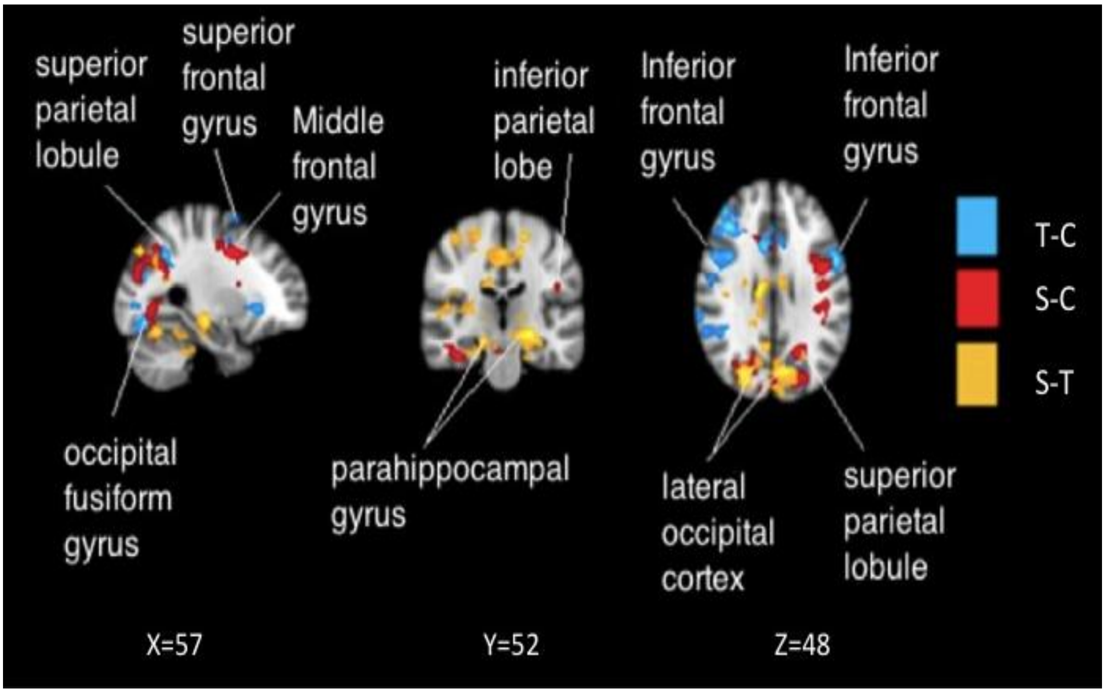
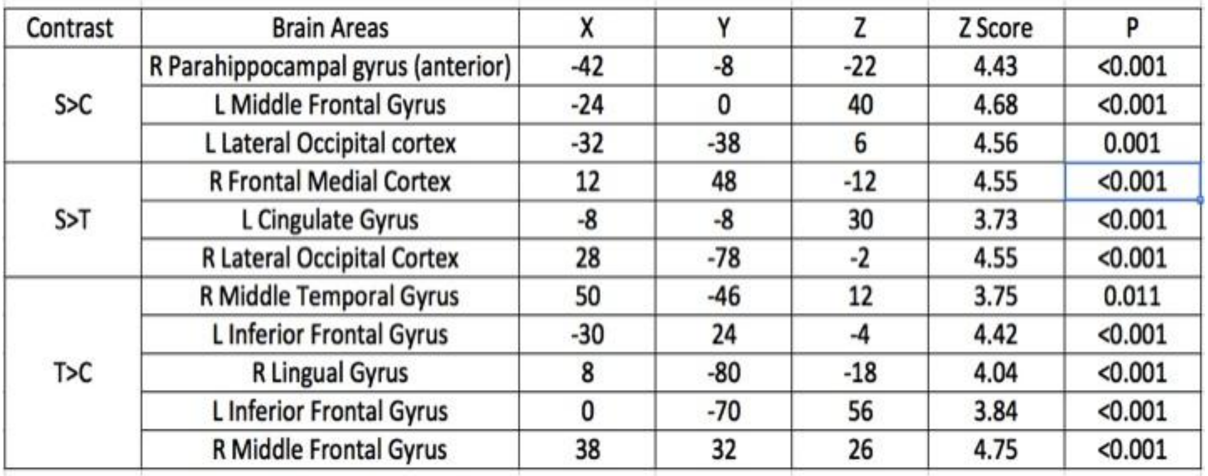


Figure 2.8. Modulation of brain activity by task (P<0.05). Three brain slices in the (a) sagittal (b) coronal (c) axial plane show modulation of brain activity by the spatial task in contrast to the feature conjunction task (red), the spatial task versus the temporal task (yellow) and temporal task versus the feature conjunction task (blue). Brain activations are overlaid on the MNI template, Images are in radiological convention (i.e. right and left are reversed). T-C = temporal > conjunction; S-C = spatial > conjunction; S-T = spatial > temporal.

Table 2.1. Areas with increased BOLD within the single task conditions. X, Y and Z denote the co-ordinates of these cortical areas in MNI space. The Z-score relates to the peak Z stat within the cluster, however the full cortical areas that these clusters covered are lablelled in figure 2.8.



Contrast	Brain Areas	X	Y	Z	Z Score	P
S>C	R Parahippocampal gyrus (anterior)	-42	-8	-22	4.43	<0.001
	L Middle Frontal Gyrus	-24	0	40	4.68	<0.001
	L Lateral Occipital cortex	-32	-38	6	4.56	0.001
S>T	R Frontal Medial Cortex	12	48	-12	4.55	<0.001
	L Cingulate Gyrus	-8	-8	30	3.73	<0.001
	R Lateral Occipital Cortex	28	-78	-2	4.55	<0.001
T>C	R Middle Temporal Gyrus	50	-46	12	3.75	0.011
	L Inferior Frontal Gyrus	-30	24	-4	4.42	<0.001
	R Lingual Gyrus	8	-80	-18	4.04	<0.001
	L Inferior Frontal Gyrus	0	-70	56	3.84	<0.001
	R Middle Frontal Gyrus	38	32	26	4.75	<0.001

Spatial > Conjunction

Although activation peaked in the left lateral occipital cortex, the activation was spread bilaterally across the right and left intra-parietal sulcus. The second cluster also peaked in the left middle frontal gyrus but extends across to the right middle frontal gyrus. The third main cluster peaked in the right parahippocampal gyrus.

Spatial > Temporal

Unlike spatial>conjunction, a contrast between the spatial and temporal task led to significantly less frontal cortex activation. Although a cluster of activity was observed in the right front-medial cortex, frontal activation was restricted to this area. Occipital lobe activation peaked in the right LOC, however similarly to the spatial>conjunction task, the BOLD clusters spread bilaterally across the left and right IPS. A third cluster was also observed in the left cingulate gyrus.

Temporal > Conjunction

Unlike the spatial>temporal contrast, this contrast revealed substantial frontal cortical activation. Clusters peaked at the right and left IFG, and right middle frontal gyrus. Localisation of the peak voxel is reported in Table 2.1 however the clusters were more widespread. Clear lateralisation of activity was not observed: in the left hemisphere, activations were seen in the SFG, IFG and the SPL. In the right hemisphere, activations were observed in the right TPJ and the right IFG, MFG, SFG and right lingual gyrus.

Activations associated with explicit feature conjunction

Two statistical contrasts were undertaken to observe task specific activations that correlated with the conjunction task in contrast to either the spatial task or the temporal task. No significantly activated voxels were detected with either the conjunction > spatial contrast or the conjunction > temporal contrast.

Chapter 5

In the introduction section you sought explanation around:

- spontaneous integration that has been shown to last up to 4 seconds
- The explanation around the study carried out aby Keizer et al. ,2008.
- You also didn't like my inconsistent use of V5/MT (MT/MST). I have corrected this throughout the thesis to V5/MT.
- You had noted several points of confusing surrounding my retinotopic mapping data acquisition section. This is now on page 135 and has been broken down to explain the percentage signal change analysis that was carried out on the data. I have also inserted the equations that were used to calculate the IFCC/RFCC in the behavioural data and the percentage signal change in the ROI - V5/MT.
- In the results section the two correlations that were carried out were not consistently formatted. This has now been corrected on page 144 and 145.

Chapter 6

You looked for explanation around the Smith et al. (2004) study on page 119 of the submitted thesis. This has been expanded on page 166 of the second thesis submitted.

2.4.1 Dual Tasks

Six contrasts were calculated when contrasting each dual task against each other. However, only three contrasts yielded significant activation clusters. These are presented in Figure 2.6.

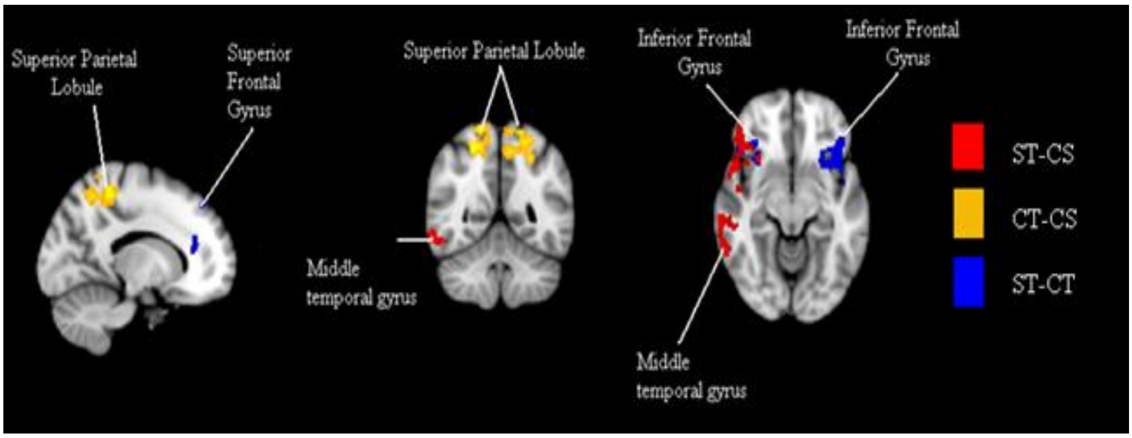
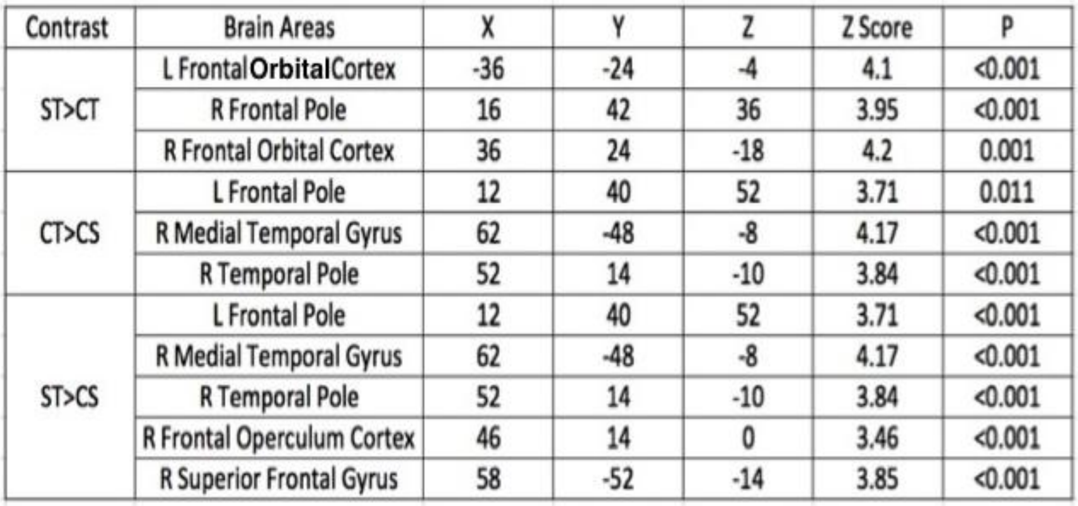


Figure 2.9. Areas within the brain that show significant clusters of activation during the dual task conditions. Brain activations are overlaid on the MNI template. Unlisted contrasts resulted in no significant clusters to report. The key shows the dual tasks that were contrasted against one another. For example, red indicates ST>CS, yellow is CT>CS and blue is ST>CT. As described in section 2.3 (Methods), the dual task consisted of the subject being cued to, and answering, two questions regarding the stimuli, ST = spatial/temporal; CT = conjunction/temporal; CS = conjunction/spatial.

Table 2.2. The dual task contrasts that resulted in significant activations. The anatomical location of the peak voxel is identified. Figure 2.6 illustrates the regions covered by these clusters.



Contrast	Brain Areas	X	Y	Z	Z Score	P
ST>CT	L Frontal **Orbital** Cortex	-36	-24	-4	4.1	<0.001
	R Frontal Pole	16	42	36	3.95	<0.001
	R Frontal Orbital Cortex	36	24	-18	4.2	0.001
CT>CS	L Frontal Pole	12	40	52	3.71	0.011
	R Medial Temporal Gyrus	62	-48	-8	4.17	<0.001
	R Temporal Pole	52	14	-10	3.84	<0.001
ST>CS	L Frontal Pole	12	40	52	3.71	<0.001
	R Medial Temporal Gyrus	62	-48	-8	4.17	<0.001
	R Temporal Pole	52	14	-10	3.84	<0.001
	R Frontal Operculum Cortex	46	14	0	3.46	<0.001
	R Superior Frontal Gyrus	58	-52	-14	3.85	<0.001

Note. **The coordinates are shown in MNI space. ST = spatial/temporal; CT = conjunction/temporal; CS = conjunction/spatial; L = left; R = right. Z –Score is equal to the peak z-stat in that cluster.**

2.4.2 Retinotopic Mapping Results and ROI Analysis

An ROI analysis was carried out on V1, V4 and V5/MT in order to test for a differential BOLD signal in associated with the feature conjunction task over and above the spatial and temporal tasks. V5/MT and V4 have been shown to preferentially process motion and colour respectively (Zeki, 1974). In order to assess the hypothesis that the formation of a feature conjunction happens in the areas that show specialised processing of the features being bound, V4 and V5/MT were defined as regions of interest using retinotopic mapping. Following this, the percentage signal change was calculated in each of these areas for each of the single task contrasts (S>C, S>T, T>C, C>S, C>T, T>S). The percentage signal change was calculated in Featquery. Featquery was implemented per participant using an individually retinotopically defined mask for V1, V4 and V5/MT. The mean percentage increase was then calculated. A one-sample t-test was then conducted to establish whether any contrast revealed a significant signal change relative to zero. Table 2.3 below shows the percentage increase in BOLD signal for each of the single task contrasts. The reverse contrasts are not listed as the BOLD increase or decrease in this case is the mathematical opposite of the main analysis.

V1

V1 responded more strongly during the spatial detection task, over and above the conjunction and temporal tasks: S>C led to a significant increase in the percentage of BOLD signal, t(16)=2.709, P=0.008, as did S>T, t(16)=2.584 P=0.015, however, T>C did not lead to a significant BOLD increase, t(16)=-1.186, P=0.254.

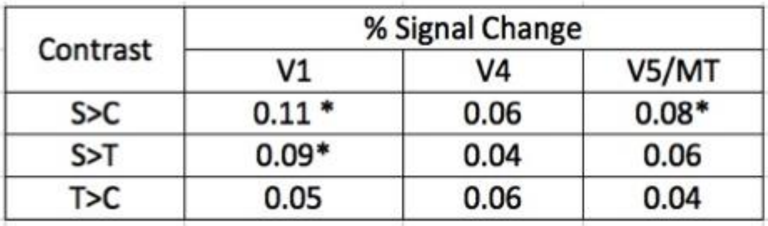
V5/MT

V5/MT showed an overall preference for the spatial task in contrast to the feature conjunction task. S>C led to a significant increase in the percentage of BOLD signal, t(16)=2.541, P=0.023, as did S>T, t(16)=1.504, P=0.153. T>C did not lead to a significant increase in BOLD, t(16)=-1.035, P=0.1585.

V4

V4 did not show a significant change in BOLD, for any of the single task contrasts. (all t<2.0, all p> 0.05).

Table 2.3. Mean percentage increase in BOLD Signal for each single task contrast.



Contrast	% Signal Change		
	V1	V4	V5/MT
S>C	0.11 *	0.06	0.08*
S>T	0.09*	0.04	0.06
T>C	0.05	0.06	0.04

Note. **The * denotes the contrasts that were significantly different from zero. S-C = spatial minus conjunction; S-T = spatial – temporal;; T-C = temporal minus conjunction; MT = medial temporal; MST = medial superior temporal area.**

2.5 Discussion

The main aim of this experiment was to seek evidence for a neural substrate of explicit, task-relevant feature binding by measuring the BOLD signal change associated with discrimination of spatial location, temporal order or feature conjunctions. Crucially, both the sensory stimulus and the motor response demands were held constant throughout the experiment, permitting a direct comparison of task-related cortical activity which is not confounded by variation in stimulus characteristics. The dual tasks triggered a significant increase in difficulty relative to the single tasks; consequently the dual task analysis was restricted and dual tasks were contrasted to one another.

Single Tasks

The single task analysis led to 6 main contrasts being calculated (S>T, S>C, T>C, T>S, C>T and C>S). Each single task was compared to every other, leading to a more thorough approach and addressing contradictions present in the literature surrounding temporal attention (Battelli et al. 2007) as well as the role of cortical areas associated with spatial detection and explicit feature conjunction judgements.

The contrasts designed to isolate unique activation associated with the feature conjunction task (C>S and C>T) revealed no significant clusters of activity in either contrast, and no significant increases in activation within the pre-defined ROIs. There at least two possible explanations for this negative finding. First, it is possible that there are no unique anatomical substrates for feature binding, and that the neural processes permitting explicit (task-relevant) feature conjunctions are subsumed within cortical networks that oversee spatial and temporal decision-making. Second, since the dot patches were spatially distributed across the visual display, it is possible that the conjunction task also implicitly engaged spatial attention, and that by doing so any unique activity associated with feature binding *per se* was masked. A key hypothesis of the FIT model is that attending spatially to the position of the moving dots would have led to an implicit binding of motion and colour via the mechanism of spatial attention (Treisman et al. 1980), therefore, both processes may have been evoked by the spatial discrimination task, leading to a lack of unique activations during an explicit feature binding task. An alternative explanation for the lack of unique activations observed during the feature conjunction task stems from the "integrated-competition" model (Duncan, Humphreys and Ward, 1997). A key prediction of this "integrated-competition" model is that directing attention to one feature of an object will result in the selection of its other features; not just those relevant to the task but also those features that are currently irrelevant to that task. Therefore, attending to one of the features or spatial location of those features, irrelevant of the task condition, could lead to implicit binding of motion and colour in each trial that the subject completes. If true, this explanation presents a significant logical challenge for studies of feature binding given the impossibility (in the undamaged brain) of decoupling individual visual features from their spatial reference frame.

It was clear from both spatial contrasts (S-C and S-T) that spatial discrimination elicits a large and widespread BOLD signal across the established fronto-parietal network, often associated with spatial attention. Clusters of activity were seen in the expected epi-centres of the spatial attention network; the bilateral parietal cortices, specifically the right and left IPS, and the medial temporal lobe (Kim et al. 1999).

In order to distinguish the cortical areas engaged in feature binding from those engaged during a spatial detection task, the "What?" task was contrasted to the "Where?" task. As discussed in the introduction section of this chapter, categorical relations assign a spatial configuration or a range of positions without defining the exact metric properties (such as above/below,left/right). It is thought that categorical spatial information is integral to the identification and recognition of objects. Based on the left hemispheres specialised processing of language (Springer and Deutch, 1985) and a right hemisphere dominance for navigation (De Renzi, 1982), Kosslyn et al. (1989) proposed that the left cerebral hemisphere would be involved specifically in categorical processing, whereas the right hemisphere should be more specialised in exact metric coordinate processing. In particular Kosslyn et al. (1998) argues that the posterior parietal cortex is integral for categorical spatial judgements.

Two statistical contrasts were performed to establish the areas more responsive to the spatial discrimination judgement in contrast to either the temporal judgement or the feature conjunction judgement. For the spatial discrimination task, activation was overall biased toward the left hemisphere, including the left MFG, right parahippocampal gyrus and the left LOC. An increase in BOLD in the left MFG is consistent with previous results that have been associated with categorical spatial memory (Sitnick and Moo, 2006). Furthermore right parahippocampal gyrus activity has been consistently associated with visual spatial memory (Bohbot et al. 1998; Kopelman, Stanhop and Kingsely, 1997; Johnrude, Owen, Crane, Milner & Evans, 1999). These results are consistent with the conclusion that the spatial task successfully led to the processing of categorical spatial relations. However, the parahippocampal gyrus has been suggested to play a role in maintaining bound representations, in particular bound representations with spatial associations (Piekema, Rijpkema, Fernández, & Kessels, 2010).

The documented cortical network engaged during temporal judgement tasks has been inconsistent (Davis et al. 2009; Coull et al. 1998). The structure of this experiment allowed the cortical activity associated with a temporal judgement to be observed in contrast to both spatial discrimination and a feature conjunction judgement. In contrast to the feature conjunction judgement, temporal order judgements were associated with a widespread network of activity in the left hemisphere in the SFG, IFG and SPL and the right hemisphere in the TPJ, IFG, MFG, SFG and right lingual gyrus. This These findings are inconsistent with early studies which suggested that the left hemisphere plays a more dominant role in processing temporal information (Coull & Nobre, 1999) as well as more recent studies which argue that the right TPJ shows unique activation during temporal order judgement tasks (Davis et al. 2009). As noted earlier, both of these previous experiments differ considerably from each other and with the current study in several ways. Coull and Nobre (1999) compared their temporal condition to a baseline task involving the observation of a fixation cross, whereas Davis et al. (2009) failed to control the difficulty level between the temporal condition and the feature condition.

The current model of temporal attention proposed by Battelli et al. (2007) is consistent with the notion that right and left SPL (including IPS) are specialised in spatial attention for the contralateral visual field. However, other neuropsychological and imaging studies have challenged the traditional view that the right IPL is selectively responsible for visuospatial processing (Husain & Nachev, 2007). Evidence suggests that the IPL has a crucial role in tasks that require the control of attention over time and forms one of the pivotal cortical areas in the temporal model of attention (Battelli et al. 2007; Rorden, 1997). In the current experiment both the right and left IPL including bilateral IPS were preferentially active during the discrimination of spatial location in contrast to temporal order. These cortical areas also show a significant increase in activity during a temporal order judgement in contrast to a feature conjunction judgement. These results thus support the hypothesis that the right and left IPL are involved in both spatial and temporal processing. Even so, it must be acknowledged that a shared anatomical location does not indicate a shared mechanism of action or unitary cognitive process (Chambers, Stokes and Mattingly, 2004).

The results document a consistent fronto-parietal network, engaged during spatial discrimination judgements. This finding helps to establish whether different domains of attention rely on domain specific cortical sources (Giesbrecht et al. 2003; Shulman et al. 2002; Slagter et al. 2007). While the results provide no evidence for domain specificity, studies involving transcranial magnetic stimulation suggests that parietal interference can dissociate the selection of different visual features and sensory modalities (e.g. Chambers et al. 2004; Schenkluhn et al. 2008). Here, the spatial discrimination judgement elicited a widespread BOLD signal, in contrast to the temporal and feature conjunction judgement. The bilateral activation profile associated with the temporal order judgement differed from the findings of Davis et al. (2009), which reported that the right TPJ was selectively activated during a temporal order judgement in contrast to a feature based judgement. A possible explanation for the difference in results may lie in the failure of Davis et al. to control task difficulty between the two conditions measured; the temporal order task was evidently easier than the shape judgement. This confound was circumvented in the current experiment by matching the difficulty levels as closely as possible across task conditions. Furthermore, Davis et al. (2009) compared the temporal task to a feature judgement, whereas the temporal task in this paradigm was contrasted to a feature conjunction judgement.

Retinotopic Mapping

In the whole brain analysis, the explicit feature conjunction condition did not produce any significant clusters in contrast to the spatial judgement or the temporal judgement. It was hypothesised that attending to the conjunction of colour and motion would yield a specific increase in BOLD in the feature specific areas V4 and V5/MT. However, ROI analyses did not reveal this and instead, V1 and V5/MT showed an increased level of BOLD during the spatial discrimination task and a lack of differentiation between all three tasks in V4. The retinotopic data complements the recent literature review (Roe et al. 2012) arguing that areas such as V4 and MT are not as specialised and modular as initially believed based on the pioneering work of Zeki (1973, 1983). As the visual cortex is organised in a retinotopic fashion, it is not surprising that spatial information is especially important within early cortical areas.

As a mid-tier cortical area in the visual ventral stream, V4 is believed to be important for object recognition and characterised as a colour area by Zeki (1973, 1983). However, subsequent studies also reported prominent orientation selectivity of V4 neurons (Mountcastle et al. 1987; Schein et al. 1982; Van Essen & Zeki, 1978), leaving the overall role of V4 uncertain (Roe et al. 2012). It has recently been suggested that V4 circuitry has the unifying role of enabling “selective extraction”. Roe et al. (2012) argue that our perceptual system is continuously confronted with much more information that it can actively deal with, therefore the processing load is reduced by selecting a fraction of the incoming information for deeper scrutiny. This “selective extraction” can be via bottom-up feature-specified shape or by goal-directed spatial or feature defined attention. This is supported by the current results showing that V4 did not differentiate between the spatial, temporal or conjunction task; suggesting that it may have played a more general role in all tasks in a “selective extraction” capacity.

Due to the established role of V5/MT in motion perception, it was hypothesised that during the feature conjunction judgement, an increase in BOLD in area V5/MT would be observed. However, the data showed that the V5/MT area was selectively responsive to the spatial discrimination task. A possible explanation may lie in the fact that, despite exhibiting coarse retinotopy, V5/MT does represent precise positions of objects in the visual field (Fischer et al. 2011). These results do not support the proposition by Battelli et al. (2007) that V5/MT plays a functional role in processing temporal information. In direct contradiction to the model presented by Battelli et al. (2007) area V5/MT did not show a significant increase in BOLD in response to either the temporal task or the conjunction task. Theoretically, the BOLD response from area V5/MT could have become saturated, which is to say that the neurons in V5/MT were stimulated during each trial due to the implicit processing of motion. If so, a dissociable BOLD response in area V5/MT would not have been expected in response to the temporal, spatial or conjunction task; however, a significant increase of BOLD in this region was observed during the spatial discrimination task relative to the feature conjunction task. McGraw, Walsh and Barrett (2004) recently used TMS to show that motion and positional information interact in area V5/MT. Other studies also support the hypothesis that the processing of motion in area V5/MT has a spatiotopic component (Ong, Hooshvar, Zhang and Bisley, 2009). Alongside the consideration that V5/MT may have been at least partially saturated due to implicit processing of motion, this may act as an explanation as to why V5/MT showed preferential activation during spatial discrimination judgements.

Dual Tasks

To ensure that the tasks were attentionally demanding and thus likely to yield widespread cortical activity, the single task conditions were also combined into dual task conditions. As noted previously, it was decided to increase attentional load using a dual task manipulation rather than raising the perceptual difficulty of the single tasks, because the ceiling level of difficulty had already been reached during thresholding for some participants. Perceptual discriminations were made correspondingly easier in the dual task condition in an attempt to maintain accuracy at 70%. Theoretically, this would have rendered the dual task conditions comparable with the single task conditions; however, the behavioural results during the MRI scanning session revealed a significant (10%) residual difference in the accuracy of response during the single task conditions compared with the accuracy of response in the dual task conditions. Consequently, while the dual tasks conditions can be compared with each other, a BOLD contrast between the single task and dual task conditions would be inappropriate due to this unforeseen confound of task difficulty.

Consistent with the results of the single task conditions, no cortical regions demonstrated a significant increase in BOLD when completing a feature conjunction judgement in contrast to a spatial or temporal based judgement. Thus there was no evidence for a unique neural signature of activation associated with explicit feature binding when contrasted to discrimination of spatial location or temporal order.

Two large clusters of activation demonstrate that the right and left IFG are especially activated by the specific combination of the spatial and temporal tasks. Activity observed in this area is consistent with the hypothesis that this region plays a key role in both task switching (Monsell, 2003), integration of bottom-up, sensory information and top-down response related information (Hampshire, Chamberlain, Monti & Duncan, 2002), and therefore providing an extension to the findings of previous studies. Unique activation in this area also suggests that carrying out the spatial and temporal task together may have required more inhibition and cognitive flexibility than carrying out a spatial or temporal task alongside a conjunction task. A reason for this could stem from an earlier observation: attending to the spatial location of a feature allows the conjunction of features to be encoded at no extra attentional cost. However, a temporal judgement and spatial detection task employed explicitly separate cognitive processes and therefore may require an increased level of task switching and cognitive flexibility.

In summary, the data presented here supports the notion of a ‘when’ pathway involving areas traditionally associated with spatial attention. However, a limitation of fMRI statistical inference is that the areas of BOLD observed are specific to the statistical contrast that is calculated. No evidence of temporal based functional specificity was observed in contrast to spatial detection judgement. Yet, when the temporal task was contrasted to a feature conjunction judgement, significant areas of cortical activation were observed in both the bilateral parietal and temporal cortices; further supporting previous literature (Battelli et al. 2007; Davis et al. 2009). This ambiguity might be resolved by adopting an alternative multivariate approach that circumvents the (arguably simplistic) logic of subtractive inference in univariate fMRI analysis. As previous studies have shown, univariate analysis often leads to negative findings when contrasting conditions that are highly similar (Seymour et al. 2010). But using multivoxel pattern analysis (MVPA), which enables the classification of distributed activity patterns, Seymour et al. revealed evidence of feature conjunctions within the visual cortex, as early as V1.

As noted earlier, feature binding is often observed as a spontaneous process that happens implicitly on observing an object. A clear dissociation between implicit feature binding and explicit feature binding was observed in a study by Kanwisher, (1998). Kanwisher studied patient R.M, whose condition was previously discussed in both Chapter 1 and the Introduction to this chapter. When presented with two coloured letters side by side, R.M. was at chance level (50-50) at reporting the correct letter with the correct colour. This suggested that R.M. was no longer able to bind features coherently. In a previous study, Friedman-Hill et al. (1995) concluded that due to the obliteration of the representation of space in R.M.'s parietal cortices, there was no spatial reference on which to 'hang' each feature, and so features became mis-bound and incorrectly reported. However, following this, Kanwisher (1998) carried out the same task but measured performance in an implicit reaction time task, results showed that although the patient was unable to accurately report the correct colour and letter pairing (e.g red T and a green S), the correct colour-word bindings were represented in his visual system. These results show a dissociation between implicit binding and suggest that the parietal lobes may be critical for explicit but not implicit feature binding.

Further evidence has also shown that not all features are processed equally. Chen (2009) showed that attending to the colour of an object leads to the involuntary processing of the location information of that object. However, attending to the location of that object does not necessarily lead to the processing of non-spatial features of that object, such as colour, especially when the non-spatial features are not task relevant. This serves as a possible explanation as to why the current experiment revealed a lack of significant difference between the BOLD signal during the spatial conjunction judgement and the feature conjunction judgment.

In order to measure the network associated with visual feature binding it may be necessary to employ a paradigm in which feature binding can be measured implicitly. The measurement of implicit feature binding allows the impact of the binding process to be observed and forms the focus of the remaining four chapters of this thesis.

Chapter 3

Experiment 2A and 2B

3.1 Introduction

Implicit feature binding and the formation of object files

Visual information processing occurs in a distributed fashion; that is, different features of objects are processed in anatomically and functionally distinct cortical areas (Zeki, 1976). Given that object processing is based on neurally distributed codes, a mechanism must be in place that integrates the codes representing the perceptual features that belong to that object (Treisman, 1996). Integration of information is integral to preserve object continuity throughout change, movement and obstruction, however, the mechanism by which the brain achieves this task remains unclear. There have been many proposed answers to this question, with several researchers arguing that spatial attention is the mechanism by which the brain binds features together to form perceptual objects (Hoffman & Nelson, 1981; Kahman & Treisman, 1984; Posner, 1980; Treisman et al. 1982).

It was traditionally believed that visual attention operated within a spatial reference (Treisman, 2006; Tresiman & Gelade, 1980); however, while there is little doubt that space plays an integral role in visual selection (Cave & Bichot, 1999; Lami & Tsal, 2001), it is now clear that space is not the only frame of reference in which attention operates. Much evidence has been gathered demonstrating that objects, as the unit of attention, can modulate the distribution of attention (Chen, 2000; Kramer, Weber & Watson, 1997). A seminal fMRI study carried out by O'Craven, Downing and Kanwisher (1999) took advantage of the distinct cortical processing areas within the visual processing stream in order to test key predictions of the object-based theory of attention. The aim of their experiment was to test the proposition that pre-attentive mechanisms segment the visual array into discrete objects, groups or surfaces, which then serve as targets for visual attention (Driver Baylis, Godrich & Rafal, 1994; Duncan, 1984; Vandenberghe et al. 1997).

As explained in some detail in Chapter 1, O'Craven et al. (1999) employed fMRI to investigate the units of selective attention. The stimulus used was made up of three elements: a face, a house and the direction of motion.The face and the house were superimposed on top of one another and either the house or face would move in one of four cardinal directions. The functionally dissociated nature of the three distinct cortical areas within the visual processing stream allowed O'Craven et al. (1999) to measure the level of processing of each element of the display, from the measure of the BOLD signal from each visual processing area (processing of faces - FFA, houses -PPA and motion - V5/MT). During a typical trial, either the house or the face would move in one of four cardinal directions; however, it was only the direction of motion that was task relevant. As all three attributes occupied the same location, it was hypothesised that if space was the unit of selective attention, then there should be an equal level of BOLD increase within each processing hub. However, if attention were able to exclusively select motion as a feature, it would be expected that only V5/MT would show a significant increase in BOLD. A third hypothesis postulated that if objects were the unit of selection, then attending to the motion of a house or face would lead to attention also spreading to the part of the stimulus that was moving. This would lead to the integration of the face or house with the direction of motion to form an object. If the house/face did become integrated with the direction of motion it was predicted that a significant increase in BOLD would be observed in both area MT and PPA/FFA respectively. In contrast, the cortical area associated with the processing of the non-moving part of the stimulus was predicted to show a non-significant change in BOLD siganl.

Results confirmed the latter hypothesis and demonstrated that during trials when the participant was attending and responding to the motion of a house, the BOLD signal was enhanced not only in V5/MT but also in the PPA area; whereas there was no significant change in the BOLD signal in the FFA. Similarly, when attending to a moving face, there was a significant increase in BOLD in area MT and the FFA; whereas the

BOLD in the PPA did not significantly differ. These results cannot be explained by theories in which attention solely selects either space (Treisman, 1988) or features from a scene (O'Craven, Rosen, Kwong, Treisman & Savoy, 1997; Wolfe, Cave & Franzel, 1989). This study thus supports the view that attention can operate via the selection of objects in a way that can be detected both behaviourally (Chen, 2000; Kramer et al. 1997) and neurally (O'Craven et al. 1999). The demonstrated importance of objects within the visual environment highlights the need for an object-based mechanism that underlies the encoding, maintaining and retrieval of object based information. One such mechanism proposed to underlie the immediate processing of objects is the 'object file'. Following several studies, Kahneman et al. (1992) suggested that information about objects was integrated and stored in a temporary structure that would function like a file maintaining the representation of an integrated object; this was termed the 'object-file'.

Kahneman et al. (1992) investigated the relationship between visual processing and object continuity using the object-reviewing paradigm. A typical trial consisted of a preview display (S1) with two or more letters, each in an individual frame, and a target display (S2) with a single letter in one of the frames. The task was to report the identity of the target letter as fast as possible. The results showed that RT to the target were reliably shorter when the target was a previewed letter that appeared in the same frame compared with a previewed letter that appeared in a different frame. Kahneman et al. (1992) argued that these results provided evidence for an object-specific advantage that could be observed when two objects were presented in close spatio-temporal proximity and therefore seen as different states of the same object instead of two separate objects (Chen, 2012). However, this object-specific advantage was only present when both the location and letter matched. When only the letter matched, negligible RT benefits were observed. This led Kahneman et al. (1992) to argue that it was spatial information that modulated the encoding and retrieval of an object file.

Repetition effects between two objects, presented in close spatial and temporal succession, indicates that the features no longer exist as individual features; they have become integrated. This is evidenced by the modulation of reaction time by the relationship of the task relevant feature to the other features that are present in the object.

More recent experiments have led to an evolution of the ‘object file’ model. Hommel (2004) argues that instead of a processing benefit, what is actually being observed is a partial repetition cost. Hommel (1998) has shown that there is not a significant difference between the reaction time following the repetition of all features, in contrast to the alternation of all features. Therefore, incomplete repetitions (e.g. colour match combined with a motion mismatch) lead to a RT or a ‘partial repetition’ cost, above and beyond that observed when all features change (Hommel, 1998; Hommel & Colzato, 2004). If, as Kahneman et al. (1992) argues, location is integral to the formation and retrieval of an object file, then this would mean that non-spatial matches would be insufficient to cause a retrieval of information unless they were mediated by a location match. However, although spatial information plays a clear role in multi-element displays, due to the need to track the identity of an object, it has been shown that spatially unmediated interactions between non-spatial features can, and do occur (Calzone, Raffone & Hommel, 2006; Hommel, 1998, 2007). One aspect of the reviewing paradigm overlooked by Kahneman et al. (1992) was that of motor actions. If the temporal co-occurrence of perceptual features led to a spontaneous binding of all perceptual features, it would logically follow that motor actions associated with that object also become integrated into the object file.

To answer this question, Hommel (2004) modified the reviewing paradigm and showed that the temporal co-occurrence of the object, along with an arbitrary button press, led to integration of both perceptual and motor features of the stimulus presented. This was evidenced by the partial repetition cost seen when either the colour, location, form or motor action alternated between S1 and S2 in contrast to when all features either repeated or changed.

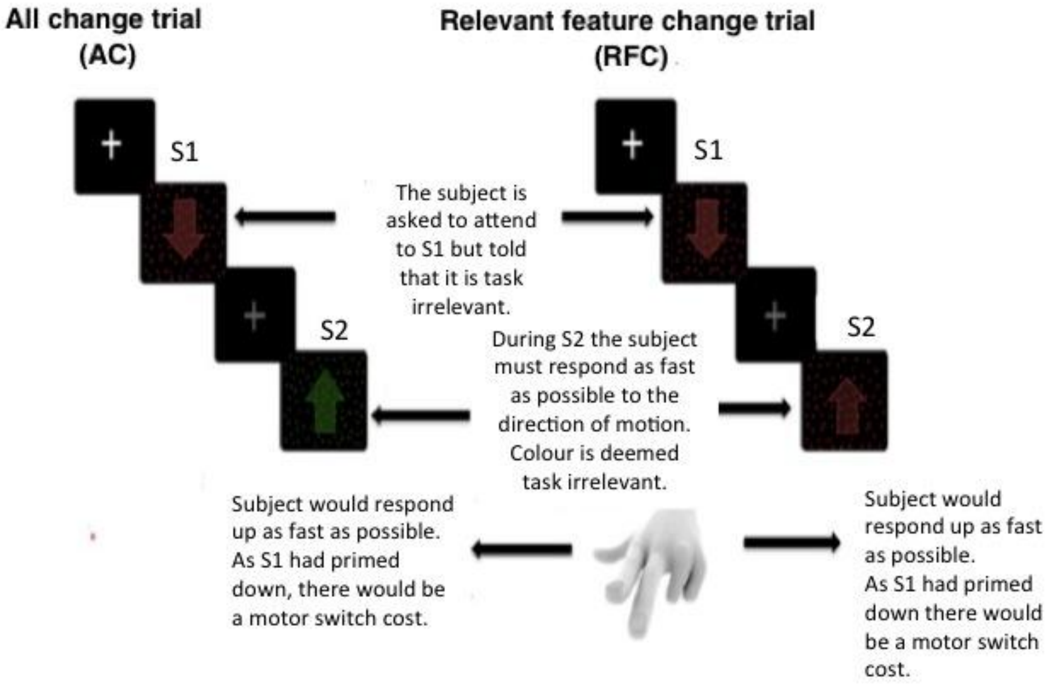
Using the reviewing paradigm, the current experiment sought to demonstrate a partial repetition cost using stimuli with two non-spatial features (colour and motion) while making location-based information obsolete by presenting the stimuli in the preview screen (S1) and the target screen (S2) across the whole screen. It was assumed that by colour and motion sharing the same location in S1, they would be integrated into an object (van Dam & Hommel, 2010).

To enable the comparison of partial repetition costs caused by either alternating the relevant feature or alternating the irrelevant feature, the task consisted of 4 conditions that represented the relationship between S1 and S2. These were: all change (AC) where both colour and motion alternated between S1 and S2; no change (NC) where both motion and colour repeated between S1 and S2; relevant feature change (RFC) where only the task relevant feature alternated between S1 and S2 and; the irrelevant feature change (IFC) where only the irrelevant feature alternated between S1 and S2.

This revision to the reviewing paradigm further allows the analysis of the contribution of the both the task relevant and task irrelevant feature to the partial repetition cost. There is much evidence that unattended features are processed and bound with the attended feature of the object (Emmanouil, Burton & Ro, 2013; O'Craven et al. 1999), leading to the irrelevant feature modulating the behavioural response to the attended feature (Melcher, Papathomas & Zoltan, 2001). By making the distinction between a RFC and an IFC, I was able to separate and contrast the impact of a RFC versus IFC on RT.

A further advantage of separating the trials into 4 conditions and 2 contrasts was the ability to control the previously uncontrolled confound of a motor switch cost. Switch costs are generally believed to reflect the control processes that are engaged when participants switch between two or more competing tasks (A-B) as opposed to when a task repeats (A-A). It has been shown that the presentation of an object also carries with it information about the action that the object affords (Hommel, 2002). Therefore, in the reviewing paradigm, the presentation of stimuli in S1 would not only prime the subject to the perceptual aspects of the stimuli but would also prime the subject to the action that the stimulus affords. Hommel (1998, 2004) avoided confounding stimulus repetition and switch costs by adapting the reviewing paradigm to include an arbitrary motor response (R1) on the mere onset of S1. For example, participants would press either the left or right button as soon as the stimulus appeared during S1. This button press was unrelated to S1 but was presumed to prevent the motor priming caused by the viewing of the stimuli during the viewing of S1, and hence prevent switch costs.

This experiment took a different approach and matched the response repetition/switch effects across two contrasts. The relevant change condition (RFC) constituted not only a perceptual change but also motor switch effect; this was also true of the AC. The only difference was whether all features changed or whether only one feature changed. Therefore, to calculate a true perceptual partial repetition cost that was caused by the repetition of the task relevant feature, only the RFC and the AC condition were contrasted. In the same way, response repetition effects are present in the NC and AC condition. Therefore to calculate a purely perceptual repetition cost the IFC condition was contrasted only to the NC condition. It is predicted that a significant partial repetition RT cost would be observed in both the relevant and irrelevant change condition (IFC), in contrast to the AC and NCs respectively. Participants completed two separate sessions; one attending to colour and the other attending to motion. The trial began with the preview screen presenting green or red dots, either moving up or moving down. Following a 500ms gap; S2 was presented, consisting of red or green dots moving up or down. The subject responded by pushing a button as fast as possible in response to the attended feature. For example, participants pressed left for green and right for red).



All change trial (AC)

Relevant feature change trial (RFC)

The subject is asked to attend to S1 but told that it is task irrelevant.

During S2 the subject must respond as fast as possible to the direction of motion. Colour is deemed task irrelevant.

Subject would respond up as fast as possible. As S1 had primed down, there would be a motor switch cost.

Subject would respond up as fast as possible. As S1 had primed down there would be a motor switch cost.

Figure 3.1 shows two trials from an all change condition (AC, left) and a relevant feature change condition (RFC, right). The relevant feature change cost (RFCC) would be calculated by subtracting the RT during the RFC trial from the RT during the AC trial. As both trials are matched in terms of a motor switch cost the difference in RT would be attributed to the interaction between S1 and S2. In the AC trial all features alternate between S1 and S2, according to the object file theory, in this scenario there should be no reactivation of the object file on viewing S2. However in the RFC trial there is a partial repetition between S1 and S2 and therefore viewing S2 should lead to a reactivation of the object file formed on viewing S1. The old feature conjunction is then overwritten with the new combination of features. This should lead a slower RT in the RFC condition than the AC condition. The difference will be termed the RFCC and reprsents the time it takes to overwrite a previous binding of features with a new binding of features.

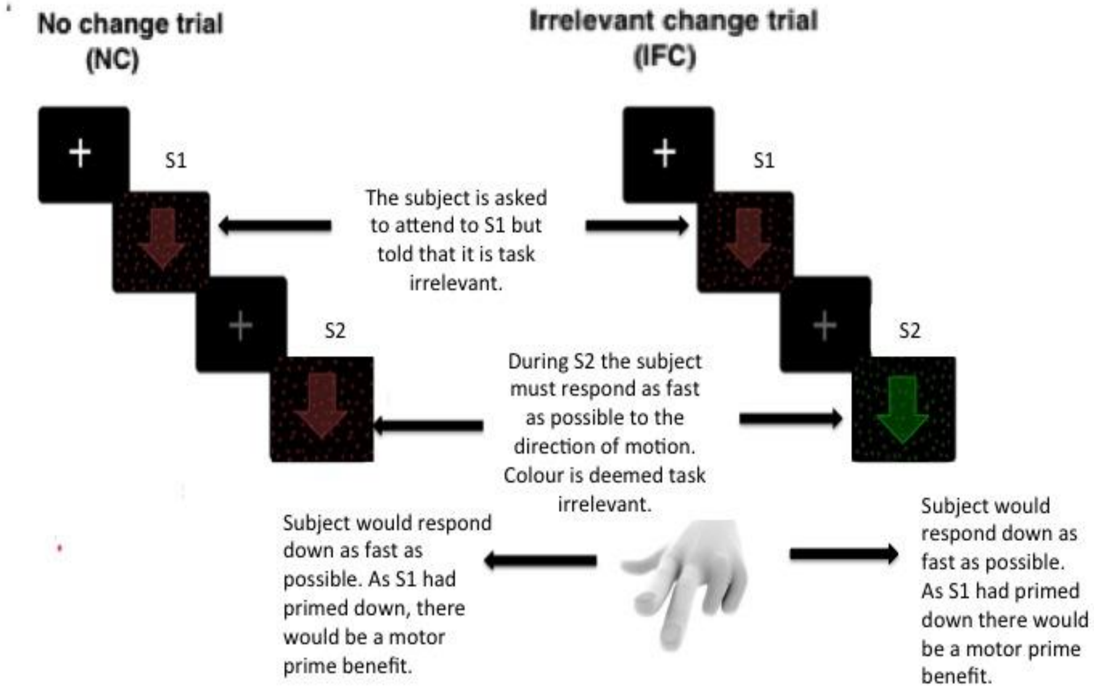


Figure 3.2 shows two trials from an no change condition (NC, left) and a irrelevant feature change condition (IFC, right). The irrelevant feature change cost (IFCC) would be calculated by subtracting the RT during the IFC trial from the NC trial. As both trials are matched in terms of a motor switch cost, the difference in RT would be attributed to the interaction between S1 and S2. In the NC trial, all features are repeated, which according to object file theory should lead to an object specific benefit (OSB). However in the IFC trial there is a partial repetition between S1 and S2 and therefore viewing S2 should lead to a reactivation of the object file formed on viewing S1. This should lead a slower RT in the IFC condition than the NC condition. The difference will be termed the IFCC and reprsents the time it takes to overwrite a previous binding of features with a new binding of features.

It was predicted that colour and motion would be integrated upon viewing S1, even though location information was made obsolete and the stimulus was made up of two non-spatial features. Following this, if either a relevant or a task irrelevant feature alternated between S1 and S2 it was predicted a RT cost would be incurred above and beyond that incurred by a complete alteration.

3.2 Method and Materials

3.2.1 Participants

30 paid volunteers (19 female and 11 male, aged 18-29 years) took part in experiment 2A. All reported having normal or corrected to normal vision and they were not familiar or made aware with the purpose of the experiment.

3.2.2 Apparatus and Stimuli

The stimulus was displayed on a 21-inch CRT monitor (vertical refresh rate of 60Hz; 1024/768 resolution; black background) at a mid-sagittal viewing distance of 50cm. Participants were asked to place their head in the chin rest and maintain focus towards the centre of the screen. Eye movements were not monitored. During the trials, participants responded by pressing either a left button or a right button on the number keypad of a keyboard centred on a desk in front of them. The stimulus was programmed on MATLAB and the results were collected at the end of each session and analysed via MATLAB.

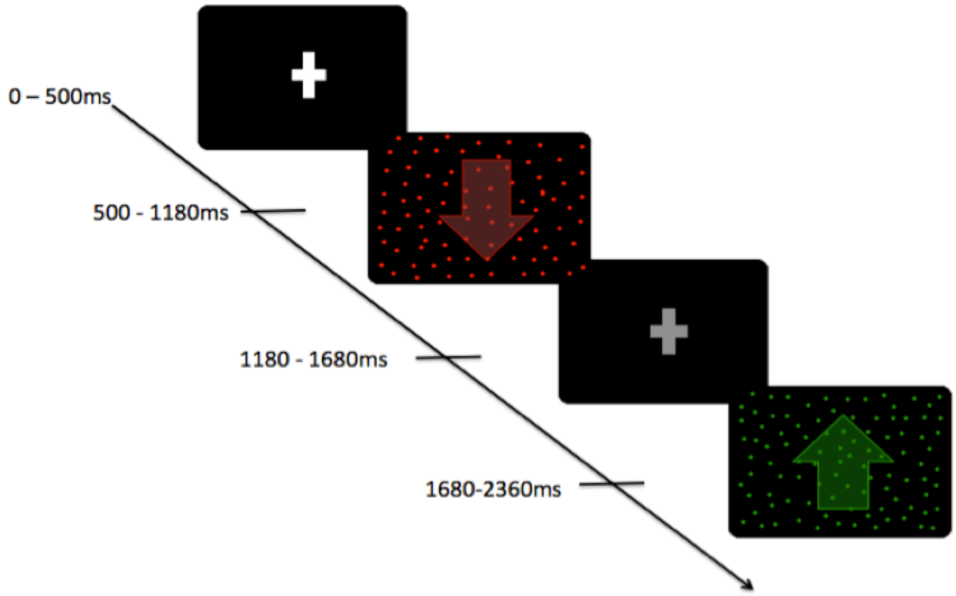


Figure 3.3. A schematic illustration of the displays and timings of events in experiment 2A. The coloured arrow superimposed on top of the coloured dots denotes the direction of motion. The stimulus is explained further below.

Screen 1 (S1) appeared for 680ms. Following this, a grey fixation cross appeared for 500ms prior to the appearance of screen 2 (S2) that was displayed for 680ms. This would equate to one full trial. The inter-trial intervals (ITI) were 2000ms and were indicated by the appearance of a white fixation cross. This was to allow perceptual separation of trial sets of S1 and S2. Participants were also advised that in-between S1 and S2 a grey fixation cross would appear. This aimed to reduce confusion about which screen they were to respond to if the participants' concentration lapsed. The dots were displayed across the whole screen. In total there were 200 dots that were all 2 pixels wide and round. The dots moved at a speed of 0.6°/s with 100% coherence. MATLAB was used to programme the stimulus and collect RT data.

3.2.3 Procedure and Design

Participants completed 2 x 1-hour sessions, carried out on 2 separate days. These were separated into a colour response session and a motion response session. The order in which the motion and colour tasks were completed was counterbalanced, leading to 15 participants completing the motion task first and 15 participants completing the colour task first.

Participants were advised that there was no connection between S1 and S2. Participants were asked to make a speeded choice during the presentation of S2. They were informed that they had 680ms to respond and any responses made after S2 had disappeared would not be recorded. In the motion condition, the subject decided as quickly as possible whether the dots were moving up or down. Participants were instructed to use the index and middle finger of their right hand to respond to the moving dots. The response mapping was balanced between participants with 50% pressing the left button to indicate upward motion and the other 50% using the right button to indicate upward motion. Participants were advised that the colour was irrelevant, that it had no relationship with the direction of motion, and hence should be ignored.

In the colour condition, participants were advised that the direction of motion was unimportant & uninformative, and hence should be ignored. In colour blocks, participants made a speeded choice at the onset of S2 as to whether the dots were red or green. As above the response mapping was counterbalanced. Instructions to participants emphasised speed, however, they were also advised that errors and missed trials would be assessed at the end of each run and the run would be repeated if the percentage of errors or missed trials was too high. Each participant completed 8 blocks over 2 sessions, with 64 trials per block totalling 512 trials. There were 128 trials per condition, with 64 in response to motion and 64 in response to colour. The order of trials was randomised at the beginning of each block. After each run, the RT was checked to ensure that the participant was not missing trials or responding too slowly. If the participant had missed more than 10 percent of trials then the block was repeated. This only happened with one participant and their performance improved on the second run. Each session consisted of a practice block of 20 randomly selected trials. Once the participant had confirmed they were comfortable with the instructions, they completed 4 experimental blocks. A short break was given after each block, where the subject could have water and relax their eyes.

As stated earlier, three equations were used to calculate the OSB, RFCC and IFCC. The mean RT was calculated for each subject during each condition. The mean for each condition was then used in the equations below:

$$\text{OSB} = \text{Mean RT during NC} - \text{Mean RT during RFC}$$

$$\text{IFCC} = \text{Mean RT during IFC} - \text{Mean RT during NC}$$

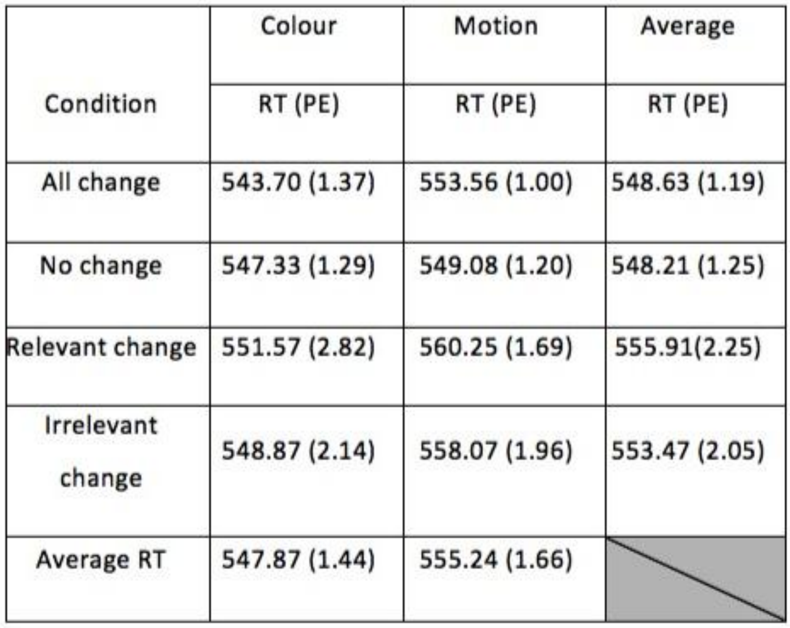
$$\text{RFCC} = \text{Mean RT during RFC} - \text{Mean RT during AC}$$

3.3 Results

In experiment 2A, the percentage of responses within the trials that were missing or anticipated (<250ms) were 2.0% and 1.3%, respectively. Trials with missing or anticipated responses were excluded from analysis. For the remaining data, which included correct and incorrect responses, mean RTs and proportions of errors (PEs) were calculated for each experiment as a function of the 4 possible relationships between S1 and S2; that is, whether all features repeated or alternated, or whether only the attended or unattended feature alternated. A 2x4 ANOVA, with repeated measures, was carried out to analyse the results. Table 3.1 below displays the mean RT across conditions in the both the motion and colour blocks and an average of both conditions.

Table 3.1.

Average RT Across Participants in msec and PE.



Condition	Colour	Motion	Average
	RT (PE)	RT (PE)	RT (PE)
All change	543.70 (1.37)	553.56 (1.00)	548.63 (1.19)
No change	547.33 (1.29)	549.08 (1.20)	548.21 (1.25)
Relevant change	551.57 (2.82)	560.25 (1.69)	555.91(2.25)
Irrelevant change	548.87 (2.14)	558.07 (1.96)	553.47 (2.05)
Average RT	547.87 (1.44)	555.24 (1.66)	

Note. Both collapsed across and within each block type and across each condition. RT = reaction time; PE = percentage of errors.

3.3.1 RT Data

A 2X4 ANOVA was carried out on the mean RT's in each of the four conditions of S1-S2 relationship (NC, AC, RFC and IFC) in two separate attended-feature block types (colour and motion). This was a two-tailed analysis because differences in either a positive or negative direction would be theoretically significant.

A 2x4 ANOVA (block type X S1-S2 relationship) revealed a significant main effect of S1-S2 relationship, F(2.62, 75.9)=5.192, P=0.002, partial η^2 =0.152 (P values adjusted using Greenhouse-Geisser). However, there was no main effect of block type, F (1,29)=0.488,P=0.509, ${}_p\eta^2$ =0.015. Therefore, there was no significant difference in RT when participants were responding to colour (M=547.8msecs, SE=8.67) or motion (M=555.23, SE=11.20) as the task relevant feature. Furthermore, there was no significant interaction between condition and block type, F(3,87)=1.28, P=0.286, partial η^2 =0.042. Analysis of simple main effects with Bonferroni correction revealed that the significant main effect of the condition was driven by a slower RT when the irrelevant feature alternated (*M*=553.46, *SE*=8.38) in contrast to the average RT when all features changed (M=548.62, *SE*=8.41), *MD*= 4.84msecs*, SE*=1.54*, P*=0.0048, ${}_p\eta^2$ = 0.383. IFCC was calculated across both the motion and the colour blocks by subtracting the average RT in the NC from the average RT in the IFC. The RFCC was calculated as above by subtracting the average RT in the AC from the average RT in the RFC. The results are displayed in figure 3.4 with the negative bars indicating a RT benefit and the positive bars indicating a RT cost. Figure 3.4 displays the RT cost or benefit collapsed across both the colour and motion blocks.

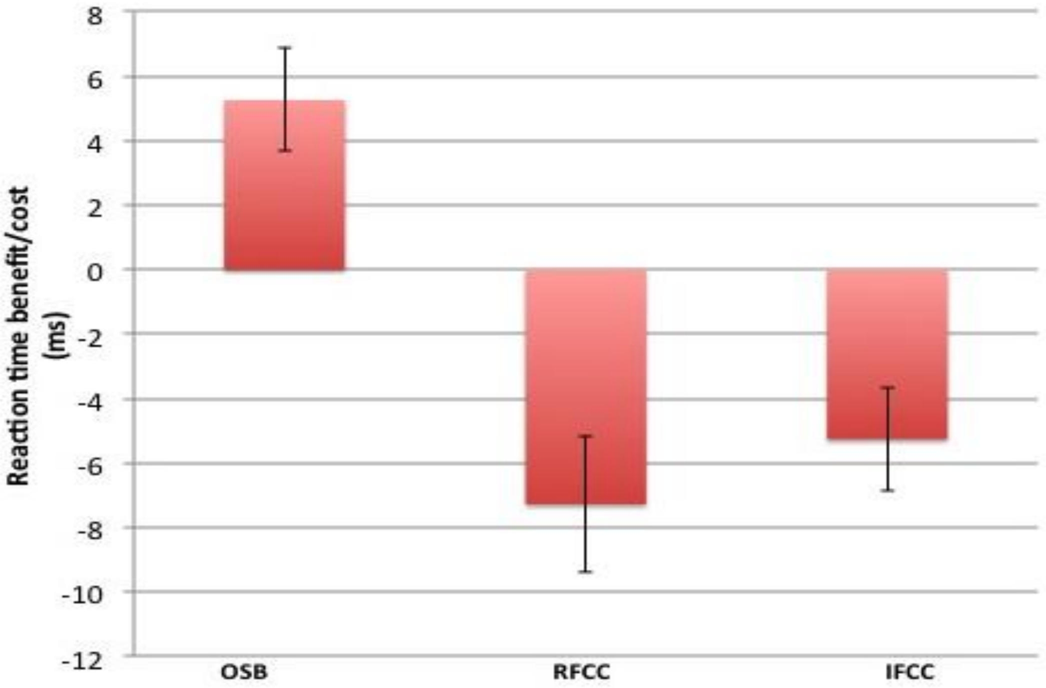


Figure 3.4. Graphical Representation of RT Benefits and Costs. RT benefit and costs collapsed across both the colour and motion blocks. Although trending in the predicted direction, neither the object-specific benefit, nor either the RFCC or IFCC RT costs reached significance; OSB = (Mean Difference =5.26ms, SE = 1.92, P=0.064, partial η^2 =), IFCC = (Mean Difference=5.26ms, SE= 1.92, P=0.064, partial $\eta^{2=}$ 0.085) and RFCC (Mean difference = 7.28ms, SE=2.74, P= 0.057, partial $\eta^{2=}$ 0.251) approach significance. IFCC = irrelevant feature change cost; RFCC = relevant feature change cost; OSB = object specific benefit. Error bars =SEM.

3.3.2 Percentage of Errors

A 2x4 ANOVA was carried out on the percentage of errors across conditions and block type. The percentage of errors is displayed in table 1. The ANOVA revealed that there was no significant difference between conditions, F (3,87)=2.27, 0.086, partial η^2=0.058. However, the ANOVA did reveal that participants were less erroneous when responding to motion (M=1.46%, SE=1.89) in contrast to responding to colour (M=1.91%, SE=0.246), F(1,29)=11.66, P=0.002, partial η^2 =0.287. There was no significant interaction between condition and block type F (2,87)=2.27, P=0.086, partial η^2 =0.073. Figure 3.5 below shows the difference in percentage error across each condition in both the motion and colour block.

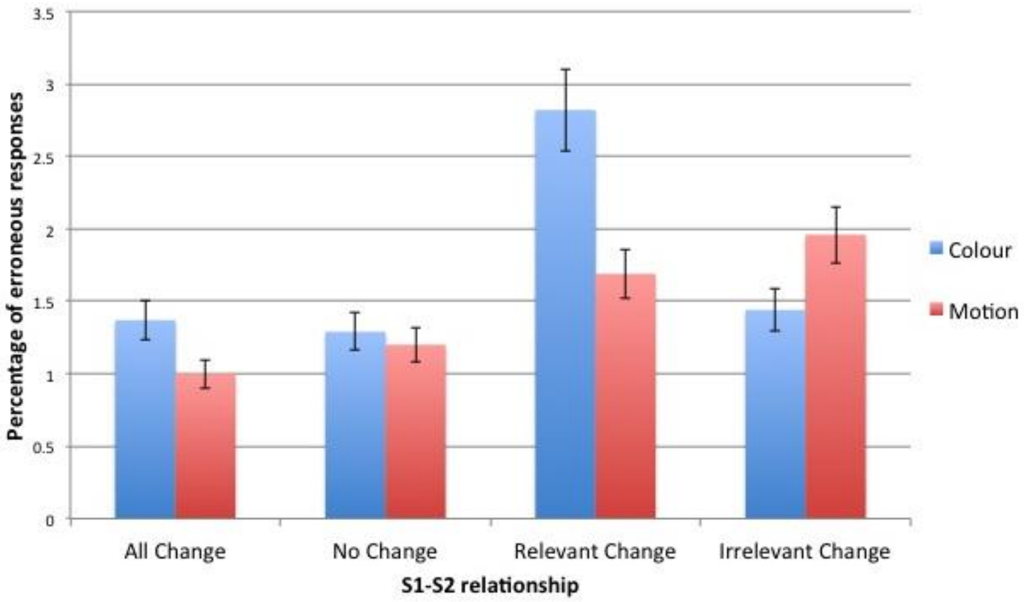


Figure 3.5 shows the percentage of error across each condition (S1-S2 relationship) when the subjects either completed a motion or colour block. There was no significant different between conditions however subjects made fewer errors when responding to motion as opposed to colour. Error bars = SEM.

3.4 Discussion

Object-specific effects and partial repetitions costs were not replicated in this study. Although they approached significance, the object specific benefit (OSB), irrelevant feature change cost (IFCC) or relevant feature change cost (RFCC) were not observed. There are several explanations as to why this result is observed.

Across the two stimuli there are overlapping features that have been ignored. These are namely shape and location. It could be argued that the lack of significant repetition effects observed in experiment 2A are due to the stimulus, presented in S1 and S2, lacking a clear 'location tag'. Kahneman et al. (1992) asserts that non-spatial matches are insufficient to cause the retrieval of an object file, unless mediated by a location match. However, a study, in which three non-spatial features (colour, shape and orientation) were manipulated while spatial location was held constant between S1 and S2, successfully demonstrated repetition effects (Colzato et al. 2006). Such results indicate that the re-activation of the representation need not be modulated by location. A pivotal difference between the stimuli used in the latter study and experiment 2A can be seen in the way that the location of the object was held constant. In contrast to the current study, where moving dots covered the whole screen on each trial, Colzato et al. (2006) presented the stimuli within a clearly defined square in the centre of a grid. Although location was held constant in both experiments, the latter format may have acted as a stronger location cue than the current stimulus, hence allowing location information to be processed and used in the formation and therefore reactivation of an object file. A further explanation may lie in another shared feature: shape. Both S1 and S2 were made up of moving coloured circular dots. This was overlooked as a possible feature that could interact with the other features of colour and motion during the processing of S1 and S2.

Theoretically, one could argue that with location and shape being held constant between S1 and S2, along with the repetition of either one of the experimental features (motion or colour), each trial could be classed as a partial repetition trial and hence may have a similar RT cost in each trial. This would have led to a non-significant difference in

RT's. However, if this was the case, a strong OSB would be predicted to be present during the NC, in which all 4 features, including location and shape, were repeated (shape, location, motion and colour). Although approaching significance (P=0.067), this was not observed.

A further explanation could be that no integration took place; therefore there was no interaction between S1 and S2 and thus no statistically significant difference across conditions. An explanation for a lack of integration may be that the stimulus did not represent an object. In an attempt to make location information obsolete, the coloured dots were presented across the whole screen. It could be argued due to the lack of coherent location information, the stimulus was not a sufficiently defined object representation in order for object-based attention to be elicited.

Following the identification of the limitations in the experimental design, the paradigm was modified in order to address these concerns. Although the results show that the data was trending in the predicted direction, with some P-values being marginally non-significant, it could be argued that the study may have been underpowered. However, In order to be comparable to other studies that had observed a partial repetition reaction time cost, 30 subjects had been chosen, therefore it was not appropriate to test any further subjects until the paradigm had been modified to take into account the identified flaws in the paradigm. Therefore, in Chapter 4 the paradigm was modified with features such as shape and location incorporated in order to increase the object like nature of the stimulus. A further question remains as to whether object files also contain semantic information. I adapted the paradigm in order to answer this queston in experiment 2b.

Experiment 2B

3.5 Introduction

Since the development of the reviewing paradigm by Kahneman et al, (1992), it has been established object files not only contain information regarding the perceptual links between features (Kahneman et al. 1992; Hommel, 1998; Hommel et al. 2004), but also contain information on an action afforded by that object (Hommel, 2004; 2008). However, it remains unexplored as to whether object files also contain conceptual information associated with that object.

Increasingly, evidence is supporting the view that perceptual recognition is multi-modal and implicitly linked with conceptual knowledge (Heusser, Tarimotimi, Awipi & Davachi, 2013; McClelland & Pring, 1991). Furthermore, it is established that exposure to a concept can facilitate the subsequent processing of the same perceptual information, even when the perceptual information is presented in a different modality than the cue (McClelland et al. 1991).

It is not established whether object files exist on a purely perceptual level; that is, whether conceptual information is integrated automatically along with the perceptual features, or whether conceptual information is something that would become integrated over time and stored in long-term memory structures. A study by Tipper and Driver (1988) examined negative priming across symbolic domains (pictures and words) where there was no structural relationship between objects. The results show that pictures that subjects ignore while attending to another picture achieve abstract levels of internal representation. Therefore, the results suggested that physical resemblance is not a necessary condition for negative priming to be observed. However, Tipper et al. (1988) assert that for priming to take place there must be a sufficient internal representation already in place. In the current experiment the stimulus that was used consisted of two main features: colour and motion. It would be expected that the subjects would have a strong representation of the colours red and green and the direction of upward and downward motion; however, it was unclear whether the colour and motion would have become integrated into an object file during the viewing of S1 and whether there would had been a strong enough internal representation of the bound features to lead to a cross domain feature integration.

The present experiment attempts to identify the level of internal representation achieved on viewing S1. To this end, repetition effects are observed between objects represented in different symbolic domains (pictures and words) that have no features in common. It has been posited that “objects are perceptions that reflect the physical properties that they represent” Anderson (1980). On the other hand, words are arbitrary representations that symbolise meaning. Therefore any repetition effects observed between words and objects must be beyond the physical level of internal representation; the object file must also hold abstract semantic information.

In order to test this the paradigm was modified so that S1 contained words that represented features, such as ‘red’ and ‘up’. S2 would then follow in the form of red or green moving dots, as in experiment 2a.

If the OSB, IFCC and RFCC depend on the low-level physical features of an object being repeated then we would not expect to see a modulation of the RT across conditions. Alternatively, if semantic representations of physical features are encoded within formed object files, and there is cross domain feature integration, we would expect to see a partial repetition cost when S2 is a partial repetition of S1, irrelevant of the physical resemblance of S1 and S2.

3.6 Method and Materials

3.6.1 Participants

The participants remained consistent throughout experiment 2A, 2B and 2C (appendix).

3.6.2 Apparatus and Stimuli

These conditions were consistent with that of experiment 2A, with the following exceptions: S1 would contain two words; one word would denote colour, i.e. RED or GREEN, and the second word would denote motion direction, i.e. UP or DOWN. In addition, the words were presented 2 degrees above and 2 degrees below fixation.

3.6.3 Procedure and Design

The procedure and design elements within this experiment were identical to that in experiment 2A. The sequence of a trial is shown below in Figure 3.3.

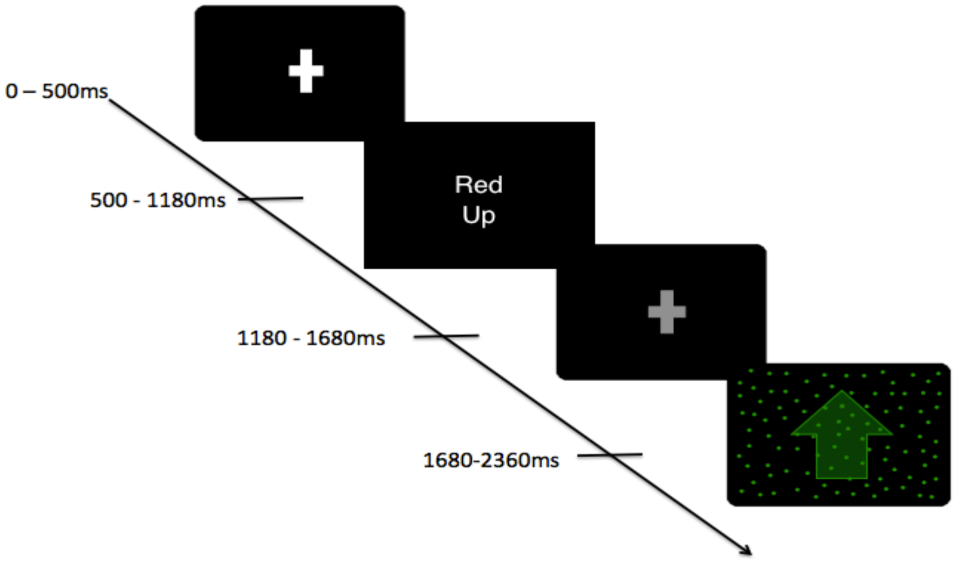
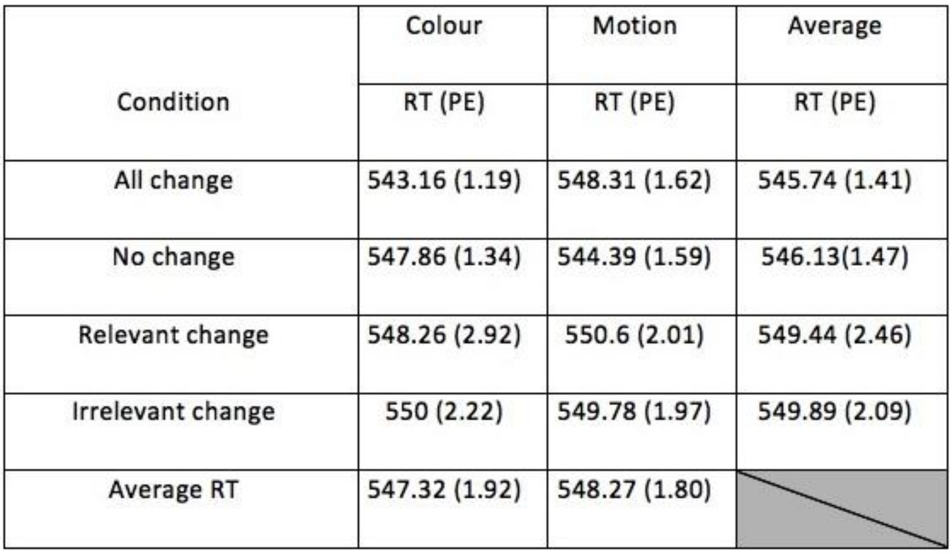


Figure 3.6. Schematic Illustration of the Display and Timing of Events in experiment 2B. S1 consisted of a combination of a colour word (red or green) and a direction word (up or down). S2 consisted of coloured dots (red or green) moving either up or down.

3.7 Results

In experiment 2B, responses were missing or anticipated (<250ms) in 1.9% and 1.2% of the trials, respectively. Trials with missing or anticipated responses were excluded from analysis. For the remaining data, mean RTs and PEs were calculated as a function of the 4 possible relationships between S1 and S2; that is, whether all features repeated or alternated, or whether only the attended or unattended feature alternated. ANOVA was performed by 2x4 ANOVA with repeated measures.

Table 3.2. Average RT Across Participants during either a colour block or motion block and an average of both (msec). Percentage error (PE) is presented in brackets.



Condition	Colour	Motion	Average
	RT (PE)	RT (PE)	RT (PE)
All change	543.16 (1.19)	548.31 (1.62)	545.74 (1.41)
No change	547.86 (1.34)	544.39 (1.59)	546.13(1.47)
Relevant change	548.26 (2.92)	550.6 (2.01)	549.44 (2.46)
Irrelevant change	550 (2.22)	549.78 (1.97)	549.89 (2.09)
Average RT	547.32 (1.92)	548.27 (1.80)	

***Note*. The average RT and PE are also displayed for block type and congruency. RT = reaction time; PE = percentage error.**

3.7.1 RT Data

The 2x4 repeated measures ANOVA with factors block type x condition revealed that condition had no main effect, F(3, 87)=1.339, P=0.276, partial η^2 =0.044. Further to this, the ANOVA revealed no significant main effect of block type, F(1,29)=0.010,P=0.922, partial η^2 =0.000, and there was no significant interaction between condition and block type, F (2.32,67.5)=1.102, P=3.53, partial η^2 =0.037. IFRC was calculated across both the motion and the colour blocks by subtracting the average RT in the NC from the average RT in the IFC condition. The RFCC was calculated as above by subtracting the average RT in the AC from the average RT in the RFC condition. The results are displayed in figure 3.4 with the negative bars indicating a RT benefit and the positive bars indicating a RT cost. The results were trending in the predicted direction but neither the RFCC (MD=3.7, SE=3.04 P=>0.99), IFCC (MD=3.76 SE=2.45, P=0.818) nor OSB (MD=-3.76 SE=2.45 P=0.818) reached significance.

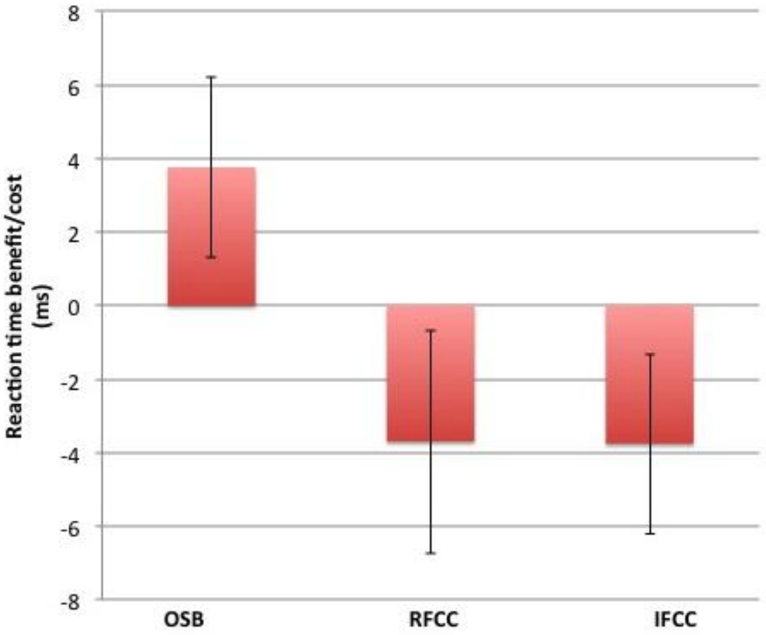


Figure 3.7. RT Benefit and Cost as a Function of Condition. Object-specific benefits (OSB = NC-IFC), Irrelevant feature change cost (IFCC = IFC-NC) and relevant feature change cost (RFCC = RFC-NC) collapsed across both colour and motion blocks in experiment 2.2. Error bars = SEM.

3.7.2 Errors

A 2x4 ANOVA was carried out on the PEs across conditions and block type. The PEs is displayed in brackets in table 2. The ANOVA revealed that there was no significant difference between conditions, F(2.25,63.10) =1.512, P=0.217, partial η^2 =0.051 (p values adjusted using Greenhouse-Geisser). Further to this, there was no significant difference in the percentage of errors between block type, F(1,29)=0.328 P=0.571, partial η^2 =0.012. The ANOVA also revealed that there was not a significant interaction between condition and block type (F (2,56.2)=1.81, P=0.150, $_p\eta^2$ =0.061.

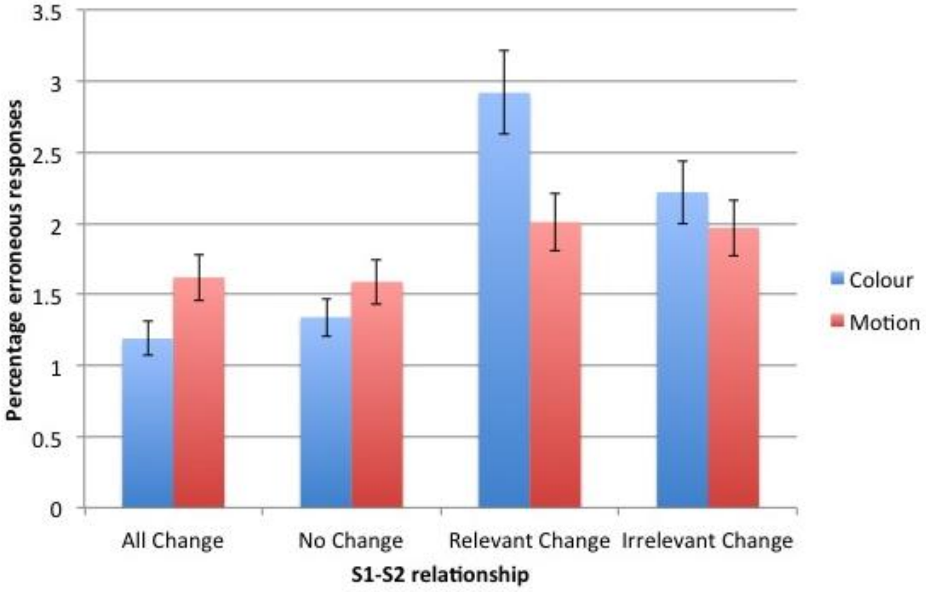


Figure 3.8 shows the percentage of error across the S1-S2 relationship condition within both the motion and colour blocks. A 2X4 ANOVA revealed that there was not a significant difference between the S1-S2 relationship conditions or the colour or motion block trials. Error bars = SEM.

3.8 Discussion

The aim of experiment 2b was to identify the level of internal representation achieved upon viewing S1 and to establish whether cross-domain binding would lead to the observation of partial repetition costs. There is evidence for binding within visual, auditory, and action related codes, as well as cross-domain bindings. However, this experiment sought to determine whether short-term integration of information into object files would also include semantic information regarding features. To answer this question, words were presented during S1 denoting colour and direction of motion, closely followed by a second stimulus (S2) made up red or green dots moving either up or down, which were either congruent or incongruent with the words presented during S1. It is clear from this experiment that the presentation of words did not disrupt or enhance RT to the target feature. The data fails to provide evidence that conceptual information is encoded as part of an object file.

Much literature supports the idea that there is conceptual priming between words and objects (Hirshman, Snodgrass, Mindes, & Feenan, 1990; Weldon, 1993; Weldon & Jackson-Barrett, 1993). This is often tested through word fragment completion tasks where the time to complete the word is modulated by the images shown to the subject prior to the task. However, the current data would suggest that the creation of object files is a purely data driven process and may be insensitive to conceptual driven effects; meaning that the object file may bind together visceral information that represents the immediate environment and semantic connections are not formed in this short-term memory formation. However, it is entirely possible that over time objects become associated semantically with other representations. Therefore, due to the timescales that both perceptual and conceptual priming operate within, this paradigm design may not be optimised to isolate conceptual priming. A study by Weldon et al. (1993) showed that, although both perceptual and conceptual priming processes can be recruited during cross modal priming between images and words it is the perceptual priming that is recruited earlier and faster. As S1 was only shown for 680ms, it is likely that the slower and less direct recovery of conceptually similar, but physically dissimilar, primes could not be recruited within the short time span available.

Further to this, the results presented in experiment 2B are consistent with neuropsychological and neuroimaging studies which suggest that there is a clear distinction within the visual system between the recognition of printed words and common objects. This is supported by neuropsychological studies that report patients with an inability to read printed words in the absence of object recognition deficits, while other forms of language-related processing are preserved (Farah, 1994). Taken together with the available evidence in the current literature, these results suggest that object files do not encode conceptual information, but act on a purely data driven basis. If conceptual information is encoded in object files, the retrieval of that information may be slower and recruited later in the recognition process. Therefore, in an experiment with an exposure time of 680ms, we would not expect to observe conceptual repetition effects. It is also possible that participants found it easier to ignore the words than the objects normally presented in S1 in previous experiments that have produced repetition effects.

Furthermore, interpreting the results of experiment 2B maybe problematic due to experiment 2A failing to produce significant repetition effects using low-level perpetual stimuli. If, as discussed in experiment 2A, the red and green dots occupying the whole screen during S2 did not lead to a integration of features into an object, then we would not expect to see object file effects such as partial repetition costs and object specific benefits in experiment 2B either. As experiment 2A, 2B and 2C were run in parallel changes to the paradigm are implemented in experiment 3 where location and shape information are introduced and controlled for in order to make the stimulus more object like.

In summary, this experiment produced no evidence to suggest that non-physical information is stored in an object file, or if it is then it is not reactivated by non-similar physical objects.

3.9 General discussion

Experiment 2a and 2b within this chapter were aimed at addressing both the non-spatial modulation of repetition effects and the wider nature of the information held in object files. Object files were considered in terms of containing information of a perceptual and semantic nature. As discussed, the failure to reproduce the established partial repetition RT costs or an object specific RT benefit, normally observed during the completion of the reviewing paradigm could be due to the stimulus presented during S1 and S2. By focusing on two non-spatial features (colour and motion), shape, as a feature, was overlooked (all dots were circular) as a contributing feature to the object formation in S1. Furthermore, the lack of location information may have either prevented an object file forming or prevented the retrieval of the non-spatial features. It has been shown previously that, for repetition effects to be observed, both S1 and S2 must be perceived as a continuation of the same object (Chen & Yeh, 2013).

A final explanation of the null results in experiment 2A is that in an attempt to make location obsolete the dots were positioned over the whole screen, which makes the stimulus less object like. If the stimulus were not perceived as an object then we would not expect to see a RFCC or an IFCC.

Experiment 2B yielded further null results. The results from experiment 2B could either suggest that conceptual information is not encoded at the object file level, or it is encoded but retrieved at a slower and later stage not captured by this paradigm.

Considered together, these experiments suggest that object file formation is highly data driven, meaning that information that may be semantically or conceptually linked with the visually present object may not be integrated, or at least not within the short time scales of temporary feature integration. Information within an object file may therefore be limited to the veridical information presented.

In order to fully explore the data, further analysis could look at the repetition cost as a function of time. Due to the large amount of trials, the stimulus may have become easier to ignore as the session progressed. If subjects were able to ignore S1 then and selectively attend to one feature in S2 then we would no expect to see any partial repetition costs. In order to modify the paradigm and make the stimulus more object like it was necessary to control for both shape and location. Furthermore, if the location was smaller and more clearly defined then the stimuli may appear more object-like and lead to integration. Therefore in experiment 3 (Chapter 4) the stimulus is modified with shape being manipulated along with location. Furthermore, the location of the stimulus is presented over is much smaller.

Chapter 4 – Experiment 3

Feature binding and the formation of object files

4.1 Introduction

The process of forming object representations and supposedly object files in visual short-term memory (VSTM) entails binding together different features of a stimulus, such as colour, shape, size, orientation, location, movement, and so forth. There has been discussion concerning the role of various categories of stimulus features within the bound objects formed. Previous research has shown that not all features are created equal, for example previous studies have shown that there is an asymmetry between the automatic selection of spatial features, such as location and the automatic selection of non-spatial features such as colour or texture (Chen, 2009).

Other studies have also shown evidence for spontaneous location processing when attention is directed towards a non-spatial feature such as colour or form (Cave & Zimmerman, 1997; Cepeda, Cave, Bichot & Kim, 1998). In order to examine the asymmetry in feature selection, Chen (2009) looked at whether the processing of an objects colour or texture automatically entails the processing of the object's location, regardless of task relevance, and vice versa. Over a series of experiments Chen (2009) showed that there was evidence of spontaneous location processing regardless of task relevance, when colour was attended. Although, processing of location was spontaneous, the degree of processing was modulated by the participant's behavioural goals, this was indicated by a larger effect when location was task relevant rather then a task irrelevant feature. However, in reverse, results showed that colour was only processed when it was a task relevant attribute. As Chen (2009) states, these results show processing asymmetry between location and colour and suggest that location selection is the default unit of attentional selection in the visual system.

Although this has been discussed extensively within the literature on visual attention and visual perception (Cave & Pashler, 1995; Cave & Zimmerman, 1997; Kim and Cave, 1995), it is unclear whether the asymmetry that is observed in visual selection tasks also apply in the formation and interaction of object files. A key difference between these studies and the reviewing paradigm is that in the aforementioned studies the target display contained several irrelevant objects. Therefore the display contained several distractors. In the experiment reported in this chapter, the target display consisted of one object. Therefore, evidence of the selection of non-spatial features will provide strong evidence for the symmetry between the processing of both spatial and non-spatial features.

Within the domain of visual perception, FIT holds that, in contrast to other stimulus properties such as colour and shape, location plays a key role in binding by providing the spatial map to which the individual features are then attached and are thus combined to form objects (Treisman, 2006; Treisman & Gelade, 1980).

Kahneman et al. (1992) proposed that it was solely the repetition of location information between S1 and S2 in the reviewing paradigm that allowed object files to be accessed and information to be used. However, it has been shown that a partial repetition of an object, caused either by a spatial feature or a non-spatial feature alternating, leads to a partial repetition cost (Hommel, 2004; Hommel & Colzato, 2004). In experiment 2A, an attempt was made to control the role of location-based information between trials by presenting both S1 and S2 over the same area. However, as we failed to reproduce repetition effects altogether, it is possible that the repetition of location may have led to partial repetition effects on each trial, hence leading to a non-significant difference between conditions. To test this assumption, the paradigm was adapted so that shape and location were manipulated along with colour and motion. Further to this, the adaptation of the paradigm also facilitated the investigation into whether each feature led to an equal IFCC and RFCC, inevitably indicating whether each feature played an equal role in the formation and retrieval of an 'object file' when present in the stimulus as either a relevant or irrelevant feature.

To do this, the stimulus was adapted so the object would alternate on 4 feature-based dimensions: shape of dot (square or circle), motion (up or down), colour (red or green) and location (left or right). In any given session, only one feature would be relevant and the other three would be task irrelevant. As in experiment 2A, trials could occupy 1 of 4 conditions: all change (AC), no change (NC), relevant feature change (RFC) and irrelevant feature change (IFC). We predicted that a RFC, irrespective of what feature that was, would lead to a partial repetition cost over and above that observed when all features alternated. Furthermore, it was predicted that an IFC would cause a partial repetition cost, although this RT cost need not necessarily be driven equally across all features. It is likely that because of a change in location being of higher salience due to the necessity to reorient attention to a new area of space, an irrelevant location change will lead to a higher RT cost than either an irrelevant colour or shape change.

Method and Materials

4.2.1 Participants

30 paid volunteers (19 female and 11 male, aged 18-29 years) took part in experiment 3. All reported having normal or corrected to normal vision and they were not familiar with the purpose of the experiment. No participants were colour-blind. All participants gave their written informed consent to the experimental procedure, which was approved by the research ethics committee at the School of Psychology, Cardiff University.

4.2.2 Apparatus and Stimuli

The stimulus was displayed on a 21-inch CRT monitor (vertical refresh rate of 60Hz; 1024/768 resolution; black background) with a mid-sagittal viewing distance of 50cm. Participants were asked to place their head in the chin rest and maintain focus towards the centre of the screen. Eye movements were not measured. During the trials participants responded by pressing either a left button or a right button on the number keypad on a keyboard centred in front of them.

The stimulus was of a similar format and identity as experiment 2A; figure 4.1 shows the structure of an ‘all change’ trial. Participants were instructed that S1 was task irrelevant but they were to passively attend to the stimulus on the screen. A grey fixation cross would then appear for 500ms (ISI), followed by the second screen (S2). Participants were asked to make a speeded choice during the presentation of S2; they were informed that they only had 680ms to respond and that any responses made after S2 had disappeared from the screen would not be recorded. Although eye movements were not recorded, subjects were asked to maintain attention towards the screen and keep chin placed in the chin rest, which ensured that they faced the screen at all times.

The stimulus was made of 4 features: colour, motion, location and shape. However only one of these features were task relevant during a block of trials. For example, in a motion block the participant was asked to attend and respond to the direction of motion during S2. The participant was instructed that all other features (shape, colour and location) were irrelevant during this block. The stimulus was displayed in an aperture that was 500 X 500, unlike experiment 2a there was now only 50 dots and they were 5 pixels by 5 pixels and moved at of 0.6°/s with 100% coherence. Dots could either be square or round, this differences constituted the shape condition. All stimuli was programmed on MATLAB.

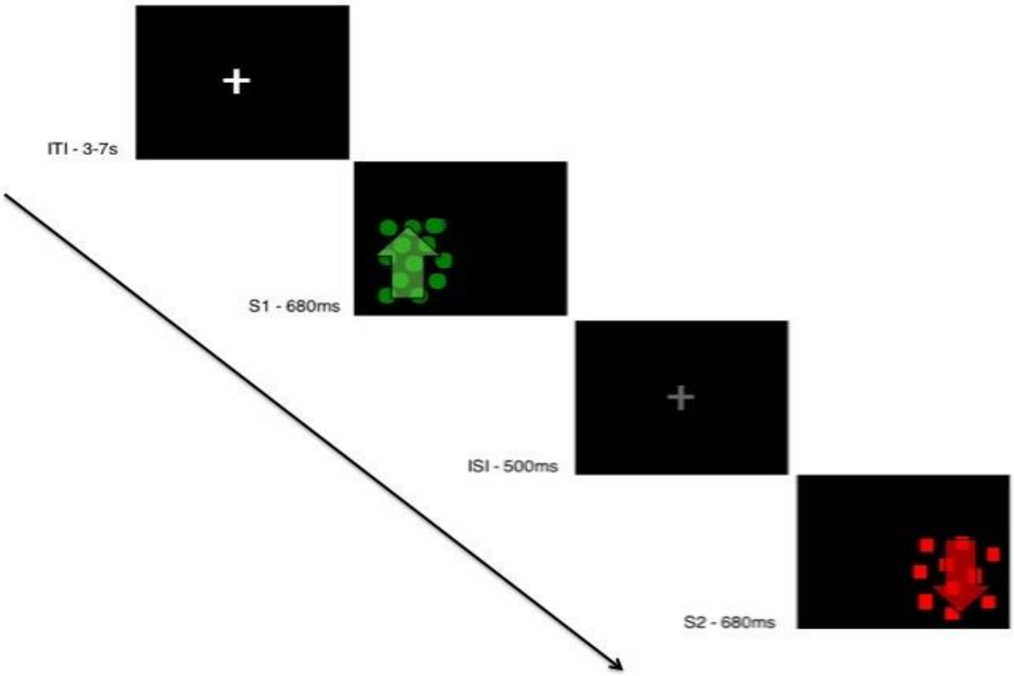


Figure 4.1. An example of an all change (AC) trial. S1 would appear for 680ms, participants would attend to this screen however they were told it was task irrelevant. Following an ISI of 500ms S2 would then appear for a further 680ms. Participants were told to respond to the direction of motion and discard all other features. In an AC trial all features would change between the presenation of S1 (green dots moving up) and S2 (red squares moving down).

4.2.4 Procedure and Design

Participants completed 4 x 1.5 hour session. For each of the four sessions the task relevant feature would be different. For example during the first experimental session the participant would complete four blocks lasting around 8.5 minutes each and they would attend and respond to motion information only. During the second experimental session the participant would complete four blocks however they would attend and respond only to location information. The final two experimental sessions subjects would attend either to only colour or only shape. The order in which the participants would complete the experimental sessions (attend colour, motion, location or shape) was counterbalanced with a latin - square design across subjects.

Each block had 128 trials, with 32 trials per condition (AC, NC, RFC, IFC). The order of trials was randomised at the beginning of each block. At the beginning of each experimental session the subject was told which feature was task relevant and carried out 50 practice trials to ensure that the correct button press was associated with the correct answer.

After each block, the RT was checked to ensure that the participant was not missing trials or responding too slowly. If they had missed more than 10% of trials then the block was repeated. This happened with just 1 participant who therefore had to be excluded. Each session consisted of a practice block of 50 randomly picked trials. Once the subject had confirmed they were comfortable with the instructions they completed 4 blocks. There was a short break after each block where the subject could have water and relax their eyes.

In order to test for repetition costs the following calculations were carried out, these were identical to those in experiment 2A and 2B. The mean RT was calculated for each condition: AC, NC, RFC, IFC and the following equations were applied:

OSB = mean RT during NC – mean RT during RFC

IFCC = mean RT during IFC –mean RT during NC

RFCC = mean RT during RFC – mean RT during AC

4.3 Results

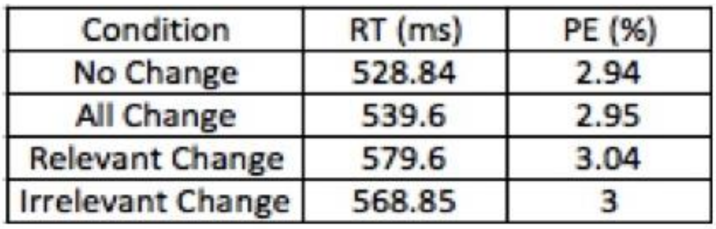
On average, across all four feature, blocks the percentage of responses that were missing or anticipated (<250ms) were in 1.8% and 0.4% of the trials, respectively. Trials with missing or anticipated responses were excluded from the analysis. For the remaining data, average RTs and PEs across all feature blocks were calculated as a function of condition. A 4x4 ANOVA (feature attended x condition) revealed a main effect of condition (F (2.2,63.8)=22.74, <0.001, partial η^2 =0.440) and a main effect of feature (F (3,87)=3.59, P=0.017 partial η^2 =0.110). There was also a significant interaction between condition and feature (F (5.59,162.29)=2.4,P=0.01, partial η^2 = 0.077).

4.3.1 Condition

The results show that there was a significant main effect of condition. As in experiment 2A, the IFCC, RFCC and OSB were calculated to test for repetition effects. These calculations are detailed in the methods section.

RFC (M=579.60ms) was significantly slower than the AC (M=539.60ms), mean difference 40ms, Std Error=6.84, P=<0.001, partial η^2 =0.541. IFC (M=568.85) was significantly slower than the NC (M=528.84) with a mean difference of 40.01ms, Std Error=7.332, P=0.005, partial η^2 = 0.323.

Table 4.1 shows the mean RT across all participants in each condition. The second column shows the mean percentage error (PE) across all subjects in each condition



Condition	RT (ms)	PE (%)
No Change	528.84	2.94
All Change	539.6	2.95
Relevant Change	579.6	3.04
Irrelevant Change	568.85	3

***Note.* RT = reaction time; PE = percentage error.**

The RFCC and IFCC were then calculated using the equations presented in the methods section of this chapter. The reaction time cost (increase in mean RT) and reaction time benefit (decrease in mean RT) is plotted below in Figure 4.2.

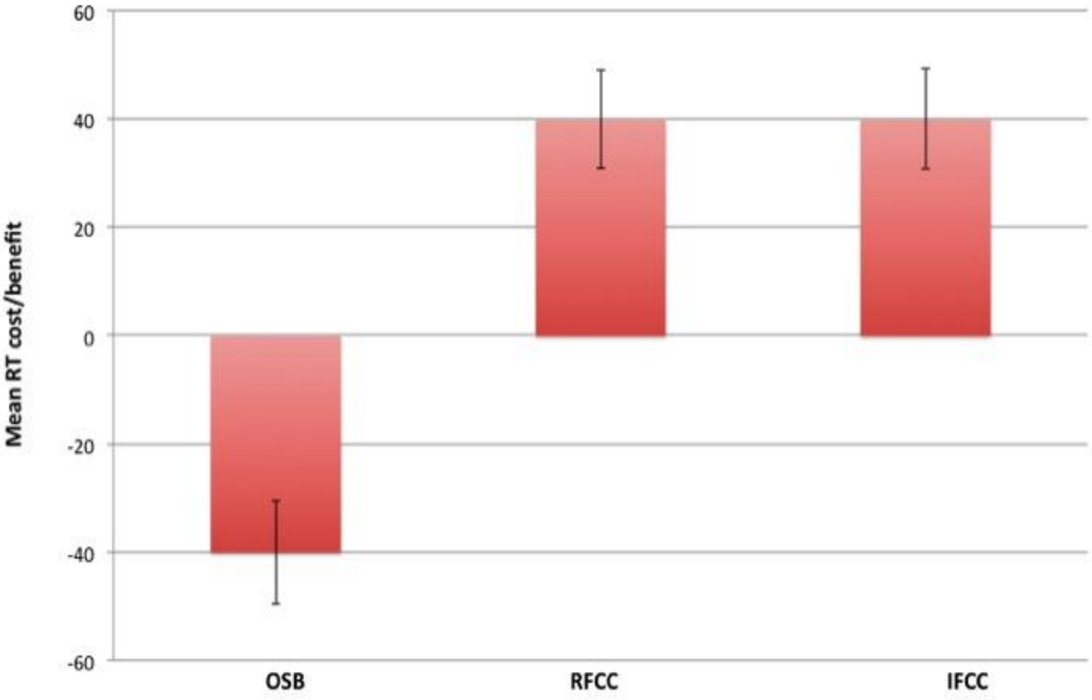


Figure 4.2. shows the relevant feature change cost (RFCC), irrelevant feature change cost (IFCC) and the object specfic benefit (OSB). The reaction time costs were calculated using the equations presented in the methods section of the chapter. The postive bars show the reaction time cost (increase in RT) and the negative bar shows the reaction time benefit (decrease in RT). Error bars = SEM

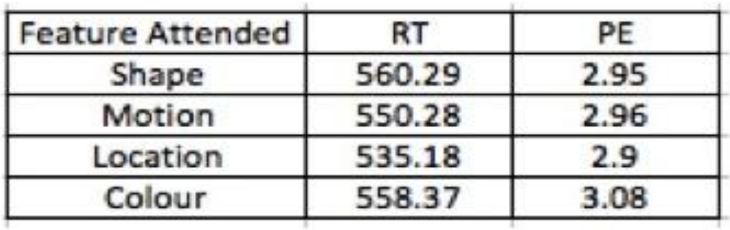
4.3.2 Feature

There was also a significant main effect of feature, F(3,87)=3.59, P=0.017 partial η^2 =0.110). Pair-wise comparisons show that, on average, participants were faster to respond to location than they were shape (mean difference = 25.11msecs, P=0.024) and colour (mean difference =23.19, p=0.034 partial η^2 = 0.253).

Condition x Feature interaction

There was a significant interaction between condition and feature, F(5.59,162.29)=2.4,P=0.01, partial η^2 = 0.077). To explore this interaction further, a 1x4 ANOVA was carried out on each feature session. This enabled us to identify any differences in the production of the IFCC and RFCC while attending to one feature.

Table 4.2. Mean RT in response to shape, motion, location or colour along with the percentage error when attending and responding to the relevant feature.



Feature Attended	RT	PE
Shape	560.29	2.95
Motion	550.28	2.96
Location	535.18	2.9
Colour	558.37	3.08

***Note:* RT = reaction time; PE = percentage error.**

Shape

A 1x4 ANOVA led the observation of a significant IFCC (mean difference =37.73ms, P=<0.001, partial η^2 = 0.318). Further to this, we observed a RFCC, which was just on the cusp of significance (mean difference = 34.18ms, P=0.054, partial η^2 =0.213).

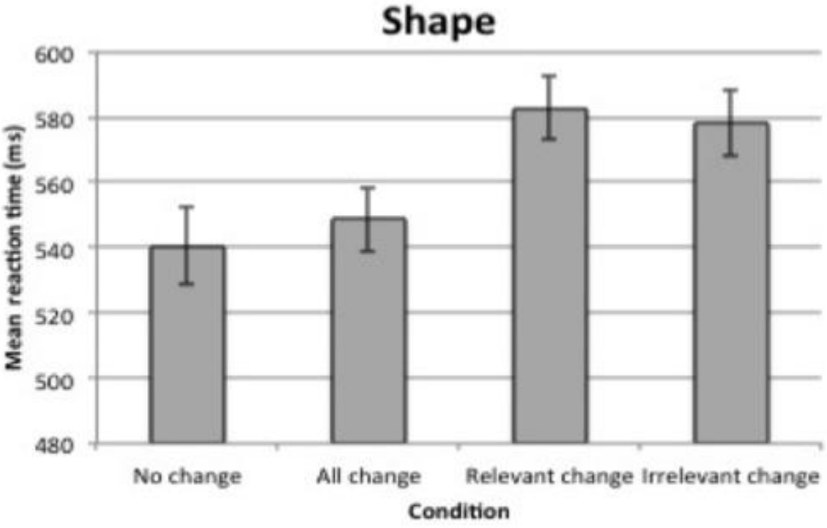


Figure 4.3 shows the mean RT across subjects in each condition. The relevant and irrelevant feature change condition led to a slower RT in contrast to the all change and no change condition. During this experimental condition subjects attended to shape. Colour, location and motion were task irrelevant features. The RFCC was calculated by subtracting the mean RT during the All Change condition from the mean RT during the Relevant Feature Change condition. The IFCC was calculated by subtracting the mean RT during the No Change condition from the mean RT during the Irrelevant condition. Error bars =SEM.

Location

A 1x4 ANOVA revealed a slightly different pattern of data. Here we saw a significant RFCC (mean difference = 53.48ms, P=<0.001, partial $\eta^2 = 0.476$) but failed to see an IFCC (Mean difference=19.24, P=>0.99, partial $\eta^2 = 0.049$).

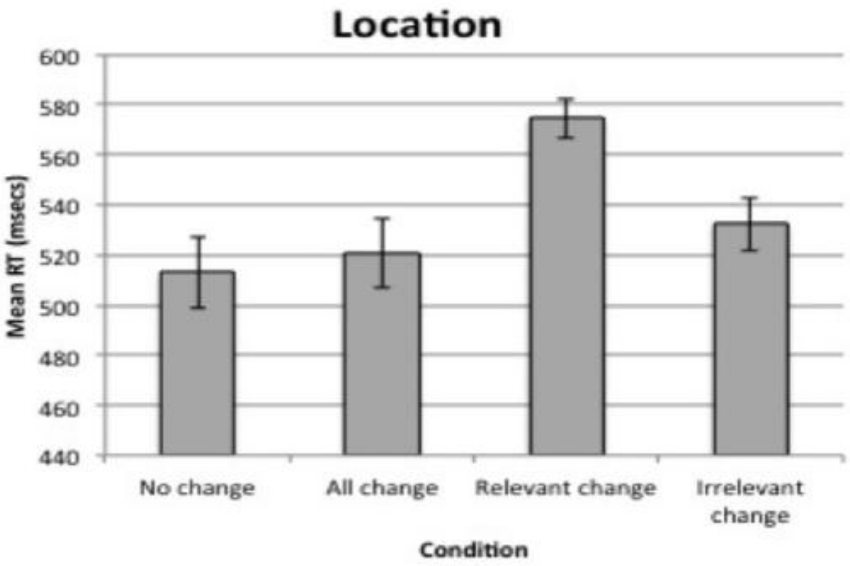


Figure 4.4 shows the mean RT across subjects in each condition. The relevant and irrelevant feature change condition led to a slower RT in contrast to the all change and no change condition. During this experimental condition subjects attended to location. Colour, shape and motion were task irrelevant features. Error bars =SEM.

Motion

Similarly to the location condition, we failed to detect an IFCC (mean difference = 2.8ms, P=>0.99, partial $\eta^2 = 0.003$) but we did observe a robust RFCC (mean difference = 35.03ms, P=0.007, partial η^2 0.308).

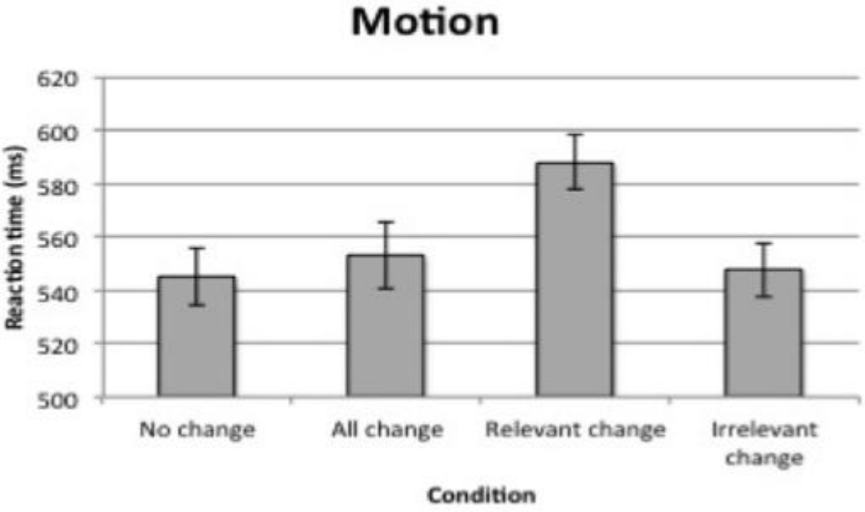


Figure 4.5 shows the mean RT across subjects in each condition. The relevant and irrelevant feature change condition led to a slower RT in contrast to the all change and no change condition. During this experimental condition subjects attended to motion. Colour, shape and location were task irrelevant features. Error bars =SEM.

Colour

A 1x4 ANOVA revealed both a RFCC (mean difference = 37.28ms, P=0.016, partial η^2 = 0.191) and an IFCC (mean difference = 57.84ms, P=0.001, partial $\eta^2 = 0.406$). This was the only feature block to show both a significant RFCC and IFCC.

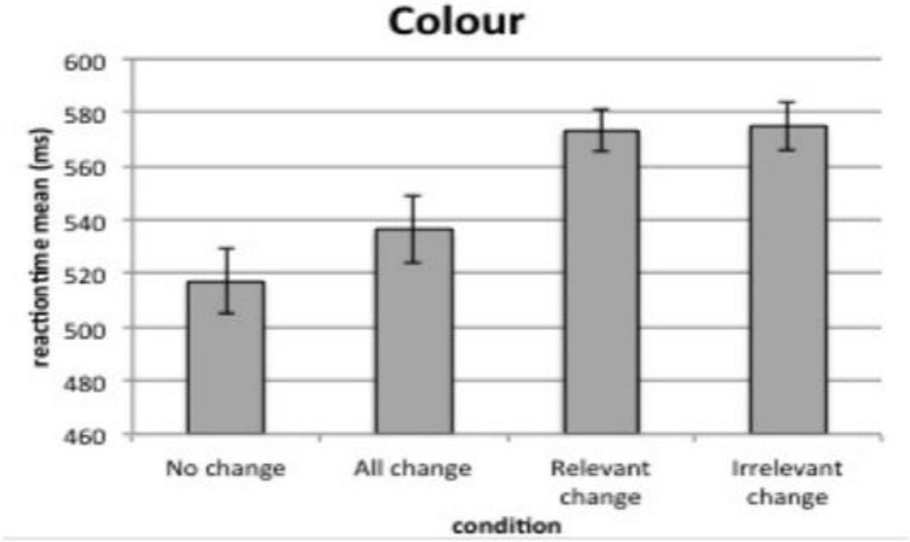


Figure 4.6 shows the mean RT across subjects in each condition. The relevant and irrelevant feature change condition led to a slower RT in contrast to the all change and no change condition. During this experimental condition subjects attended to colour. Location, shape and motion were task irrelevant features. Error bars =SEM.

4.3.3 Errors

The number of errors made across both condition and feature was analysed in a 4x4 ANOVA. The results showed that there was no main effect of condition on error rate; F (3,87) = 0.055, P=0.983, partial η^2 = 0.002. There was also no main effect of feature block on error rate; F (3,87)=0.040, P=0.989, partial η^2 = 0.001. Further to this, there was no significant interaction between condition and feature on error rate,

F (5.9,171.15)= 3.43, P=0.960, partial η^2 = 0.012.

4.4 Discussion

The present study sought to replicate established results from previous experiments showing a partial repetition cost (Kahneman et al. 1992; Hommel et al. (1998), while controlling for motor switch costs. Following from experiment 2a, where no significant partial repetition costs were observed, two key changes were made to the paradigm: firstly, both shape and location was introduced as an explicit stimulus feature and secondly, the areas over which the stimulus was presented was made much smaller. This made the stimulus much more 'object-like'.

By manipulating the to-be-attended feature of the object, we also aimed to establish whether location plays a special role within the re-activating of an object file or whether shape, motion, colour and location carry equal weight. An alternative, but not mutually exclusive interpretation of the object specific benefit (Kahneman et al. 1992), is partial repetition costs (Hommel, 1992). Partial repetition costs are incurred when one or more features are repeated, theoretically leading to the automatic retrieval of the just created binding. The RT cost is thought to reflect the cost of updating the currently held representation of an object. Partial repetition costs are thought to be the product of perceptual conflict between S1 and S2, therefore, it is less clear whether complete repetitions actually facilitate RT in the way that Kahneman et al. (1992) envisioned. The data presented here did not demonstrate a significant decrease in RT when all features were repeated between S1 and S2 in contrast to when all features alternated between S1 and S2. These findings show that full repetition held no RT benefit in contrast to a complete alteration. This is supported by previous work by Hommel (1998, 2004 & 2008) and suggests that the object specific benefit as reported by Kahneman et al. (1992) is only apparent in contrast to a partial repetition cost.

In experiment 2A, in a modest but important extension of the work completed by Hommel (1998), we measured two types of partial repetition costs against two different baselines: an irrelevant feature change cost and a relevant feature change cost. In experiment 2A, we failed to produce either partial repetition cost. However, following the inclusion and control of location and shape information, these effects have emerged. Both a RFCC and an IFCC was observed, supporting the idea that, irrespective of whether the partial repetition of an object was due to a task relevant or task irrelevant feature change, an object file was retrieved and updated. In contrast to experiment 2a, an increase in the percentage error is also seen. This suggests that the irrelevant features in this experiment were either more distracting than those in experiment 2a or participants were trying to respond faster and therefore became more erroneous. The data does not support this latter explanation, which suggests that the irrelevant features presented experiment 2a may have been easier to ignore, possibly due to the features of the stimulus not being integrated into an object.

A further point of investigation was whether location, motion, colour and shape would lead to equal partial repetition costs, either as relevant or irrelevant features in the display. The role of location information has previously been a point of contention. Kahneman et al. (1992) stress the importance of location in the creation and retrieval of an object file. However, Van Dam et al. (2010) argue that it was unclear whether RT benefits were the result of previewing a particular area of space, or previewing those features within that space. Further to this, evidence from attentional studies (Hommel 1998, 2007; Hommel & Colzato, 2004) and developmental studies (Leslie, Xu, Tremoulet & Scholl, 1998) suggest that feature bindings do not necessarily need to include spatial codes in order to be retrieved. A 1x4 ANOVA was carried out on the individual feature based blocks to enable us to see the difference in results, depending on which feature was task relevant. When location was relevant, we saw a task RFCC. However, when an irrelevant feature changed, such a shape, motion or colour, there was no significant impact upon RT. This suggests that location plays a special role and that, as long as location is repeated, an object file can be accessed with minimal cost to the perceptual system.

By looking at each feature block separately, we were able to identify differences in the way that each feature contributes to object files. When non-spatial features were irrelevant (location block), we did not see any partial repetition costs suggesting that non-spatial features can be ignored or updated with marginal cost to the perceptual system. When a non-spatial feature is task relevant, we see a different pattern of results. Attending to colour led to both a robust and significant RFCC and IFCC. Shape also showed a significant IFCC, along with a RFCC that was borderline significant (P=0.054), however with an effect size of 0.213 (partial eta- squared) suggesting that this is a partial repetition cost. However, in the motion block, we only observed a RFCC but failed to detect an IFCC. These results suggest that all features do not play an equal role, but instead task salience modulates the impact of feature alternation of object representation. Although location did produce robust IFCC and RFCC, if location information was the only way in which object files could become reactivated you would not expect to see a RFCC in any other block.

An alternative explanation for the seemingly equal role of location as a feature may lie in the fact that there was only ever one object. Episodic retrieval via non-spatial features has been demonstrated in the previous research, however, like this experiment, there was only one object (Colzato, Raffone, & Hommel, 2006; Hommel, 1998; Hommel, & Colzato, 2004). Therefore, when multiple objects are present, spatial correspondence may be integral to deal with the spatial uncertainty (Kahneman, Treisman & Gibbs, 1992; Mitroff & Alvarez, 2007; Saiki, 2003).

The observation of both the Simon effect and the spatial stroop effect have led to location being assigned an important status. The Simon effect (Craft & Simon, 1970) is observed when participants are asked to respond to a non-spatial feature in a binary choice task with a left and right assigned key response. A faster RT is observed when the key response is congruent with the side of the screen that the object appears on. The accepted view of the Simon effect is as follows: assume that subjects are responding to two letters, R and T with either a left or right button press. If the R appears on the left or response corresponding side, this stimulus will be processed along two routes. One route is under intentional control, and it is this route that acts voluntarily on task instruction. The other route is assumed to be automatic (Hommel, et al. 2004) and unconditional and connects the internal codes of spatially corresponding stimuli and responses. If the R appears on the left then both routes will become activated and therefore the left response code will reach the required response threshold quicker than in a spatially neutral condition. However if the R appears on the right, the automatic and unintentional route will activate the left response code, which in turn will lead to response conflict and delays in response execution, this is called the dual route model.

Alternatively, the object file theory offers an integration account of the Simon effect. If you apply the event file assumption that the combination of stimulus and response features in the preceding trial become integrated and are still associated with each other when the next trial begins, it is hypothesized that reactivating one member of this temporary association will also activate the other member. So if the same combination of stimulus and response features (R > Left , R >Left) were repeated, this would mean a complete match of old and new stimulus response features. This would not provide any kind of coding or selection problem, processing for these trials might be faster than control trials. Similarly no problems are expected for a complete mismatch of stimulus response features, so R = left button press preceded by a T = right button press. However, partial matches may cause processing conflicts. If, in the first trial, the letter R becomes associated with a left response, then in the following trial the R appears on the right side - a partial match results; the letter has been repeated and the location has been alternated. Therefore you would expect to see a delayed RT. Four experiments by Hommel, Proctor and Vu, (2004) showed that the Simon effect was eliminated if the preceding trial involved a non-corresponding stimulus response pairing (either a complete mismatch or complete repeat), however, following a partial stimulus-response mismatch, the Simon effect was present and robust.

Similarly, the 'Spatial Stroop Effect' (MacLeod, 1991) is observed when the subject must respond to a word that has spatial information (e.g. right or left) with a right or left key response. Although location information is irrelevant during the task, the location of the spatial word significantly modulates the RT to that word. Although, the Spatial Stroop Effect has not been examined as the Simon Effect was above it is plausible that short-term integration, as explained in the object file model, may also account for the Spatial Stroop Effect.

The current results also showed that there was significant effect of feature, meaning that participants did not respond to all features equally; attending to location did yield a faster response time than attending to shape. This suggests that location is processed at a higher speed than non-spatial features and may play an integral role in the encoding of object files. However, before a conclusion is reached it must be considered as to whether the reaction time to the four different features are comparable. It has been shown that RT to motion onset is related to the perceived speed of motion; as the speed increases the RT to motion onset decreases. The speed of the dots were not a feature that was included in the analysis or manipulated as a feature of the object. Therefore the features may not be comparable due to the different ways in which they interact with RT. In this respect, going forward this may not be a valid comparison.

The neural mechanisms underlying the impaired performance, observed after partial repetitions of objects, are unknown. It is assumed that this impairment happens due to the conflict between the retrieved and perceptually available features and/or because the old associations need to be deconstructed (Colzato, van Wouwe, Lavender & Hommel, 2006).

In summary, the results from experiment 3 support the assumption that alternating a feature of an object leads to the retrieval of a previously created binding as well as an updating of that binding. Theoretically, it is this process driving an increase in RT. Going forward, the mechanisms by which object files are formed and reviewed needs to be established. There is a lack of literature directly demonstrating that partial feature repetition indexes the retrieval of corresponding object files. By using fMRI and TMS to observe and probe the networks involved in processing features within object files, it may become clearer how the brain overcomes the monumental ‘binding problem’. To directly demonstrate that feature repetition actual indices the retrieval of corresponding object files, we need to exploit the modular processing nature of feature processing hubs and the use of fMRI as an exploration method into whether features are being reviewed and then overwritten.

Chapter 5 – Experiment 4

Exploring the neural network recruited during the formation of object files

5.1 Introduction

Due to the modular and distributed organisation of the primate brain, accurate visual perception relies on the fast integration of features (Treisman, 1996). It has been demonstrated in experiment 3 of this thesis, as well as in many other studies (Hommel, 1998; Hommel & Colzato, 2004; Kahneman & Treisman, 1992) that, when two objects are presented in close spatio-temporal succession, there is an interaction between the two objects that are captured by the reviewing paradigm. As explored in the previous chapters, a decrease in performance is observed during the reviewing paradigm if the target stimulus (S2) is a partial repetition of the preview stimulus (S1). However the neural correlates of this partial repetition cost is relatively unexplored.

The partial repetition of an object during S2 has been argued to cause conflict due to the 'reactivation' of the previously bound object (S1). Therefore, trials of this nature lead to conflict between the stored representation of an object and the newly presented representation of the object (Hommel, 2004; Kuhn, Keizer, Colzato, Rombouts & Hommel, 2010). The conflict caused by the mismatch in feature-based information is thought to lead to the automatic process of updating the object-file with the new and accurate information. It is hypothesised that the process of updating the new feature binding drives the observed partial-repetition RT cost (Hommel, 2004). Although this effect is established behaviourally, the cortical pathway engaged during this process and the underlying neural mechanisms are yet to be established. Although it has been shown that spontaneous feature integration and the immediate neural consequences of such integration can be measured with fMRI (O'Craven, 2000) and event related potentials (ERP's) (Schoenfeld, 2003), the cortical network engaged during the updating and rebinding process, which is theoretically engaged during the 'reactivation' process, is relatively unexplored.

As explained in detail in Chapter 1, Keizer et al. (2008) carried out an fMRI study using the reviewing paradigm and a stimulus made up of three types of neurally dissociable visual stimuli: faces, houses and direction of movement. Participants were presented with preview displays (S1) and targets (S2) that both consisted of blended images of a house and a face. The house or the face moved in one of two possible directions. Participants were to respond to the direction of S2, irrespective of what object moved. Of particular interest were the conditions where S1 showed a moving house and S2 a moving face; if the direction of motion between S1 and S2 were the same (i.e. the motion feature was repeated) the PPA was more active than if the motion direction alternated. Therefore, repeating the motion feature during S2 led to the retrieval of the object that moved during S1 (house) and hence led to an increase in activation within the PPA. This showed evidence that repeating a feature can reactivate the neural code of this feature, which then spreads activation to the other feature codes that it is still bound to. However, Keizer et al. (2008) failed to mirror this effect in the FFA; no significant increase in BOLD was observed in trials where the repetition of the motion direction should have led to a reactivation of the previously bound face, even though, behaviourally, the partial repetition cost was present. Due to the complex stimuli that Keizer et al. (2008) employed in their paradigm, it is difficult to interpret the partial null result. As it is established that faces are processed faster and to a much higher level than other objects (Roisson & Gauthier, 2002), one could argue that it is not unusual that the pattern of BOLD observed in the PPA was not mirrored in the FFA. As the authors themselves comment, there is evidence that stimuli of greater biological significance, such as faces, attract more attention and induce more activation (Vuilleumier, 2000; Ro, Friggel and Lavie, 2007).

The current experiment sought to explore the cortical networks associated with object files using a whole brain analysis. Through scanning the whole brain, this experiment questioned whether the ‘reactivation’ effects are restricted to the object or feature specific cortical areas (V4 & V5/MT), as per previous assumptions (Keizer et al. 2008; Kuhn et al. 2010). Using identical stimuli to experiment 3, the experiment aimed to replicate the two significant partial repetition costs in response to both an irrelevant feature alternation and a relevant feature alternation. Further to this, by separating the

RFC condition from the IFC condition, we sought to establish whether alternating a task irrelevant feature recruits the same cortical pathways that are recruited by a task relevant feature alteration. Previous experimental findings (Xu, 2010) suggest that, although the encoding of irrelevant features may be automatic and necessary, it does not mean that all features are processed equally and to the same level. Consistent with previous results (Xu & Chun, 2006) and neurophysiological findings (Toth & Assad, 2002; Freedman & Assad, 2006), Xu (2010) showed that the superior IPS seemed to process only the task relevant features, and although the task irrelevant processing of shape was indexed with an increased level of BOLD in the LOC, this quickly decayed, suggesting that the task relevant feature would be processed to a higher level. Therefore, the dissociation of an irrelevant and a relevant feature change in the paradigm will allow us to observe the possible separate neural fates of both relevant and irrelevant feature processing during the formation of object files. A further point of investigation was motivated by the hypothesis that partial repetition costs observed during object file processing reflect higher cognitive processes involved in monitoring and detecting conflicts between incoming information. Therefore, we would predict higher levels of BOLD in areas associated with conflict monitoring and resolution, such as the ACC (Botvinick et al. 2004), the supplementary motor cortex, IFG, MFG and parietal cortices (Peterson et al. 2002).

Finally, we also sought to address the question as to whether the updating of an object file with new information during S2 would lead to an area-specific increase in BOLD. This was following on from a previous fMRI study (Keizer et al. 2008) where the data showed that the right PPA, a house-selective brain area, showed increased activation to moving faces (in S2) if a couple of seconds earlier the same direction of motion had been paired with a house (in S1), compared to when both the direction of motion and the moving object alternated. The authors argue that this supports the view that the presentation of a stimulus feature (a direction of motion) reactivates features it was previously bound with (house) in an object file. Their results showed that both neural and behavioural measures were closely correlated across participants.

As discussed in Chapter 1, the authors found a similar positive correlation between the RT cost observed and level of BOLD in the FFA, however they observed a positive correlation between the RT cost and BOLD level in the FFA yet did not find the RT to be significant. This meant their results were inconclusive, however as mentioned previously, faces carry biological significance that may modulate processing in a different way to pictures of houses. The PPA and FFA were examined because they were specific to the features manipulated in the stimuli (faces and houses). In order to replicate the analysis methods of Keizer et al. (2008), two correlation tests will be carried out: firstly, between the change of BOLD in area V5/MT and the irrelevant feature change RT cost and secondly, between the change of BOLD in area V5/MT and the relevant feature change cost. V5/MT has been chosen as the studied cortical area because the attended feature in this study is motion. How the percentage signal change and RT costs were calculated is detailed in the methods section of this chapter.

We predicted that, if old information regarding the feature binding of the motion, colour shape and location had to be updated during partial repetition, then this may also be reflected in an increase in BOLD activity in the cortical areas that processes the task relevant feature: area V5/MT. If this was the case, we would expect to see a specific increase in BOLD during the RFC and IFC conditions above and beyond that seen in the NC and the AC. To test this hypothesis, we carried out retinotopic mapping on each subject allowing a region of interest (ROI) analysis to be carried out on V5/MT and the percentage signal change to be calculated. We then aimed to correlate the increase in RT with an increase in BOLD percentage change in area MT.

Previous chapters have measured 3 types of RT data: an IFCC, a RFCC and an OSB. As an OSB is the direct opposite of the IFCC measurement I no longer report this in this thesis.

5.2 Materials and Methods

5.2.1 Participants

20 healthy, right-handed participants were recruited for both parts of the experiments (mean age = 26, SD =3.8 years; 9 females). All participants had normal or corrected-to-normal visual acuity. No participants were colour-blind. All participants completed safety screening to ensure it was suitable for them to go into the MRI scanner. They gave their written informed consent for the experimental procedure, which was approved by the Research Ethics Committee at the School of Psychology, Cardiff University.

5.2.2 Apparatus

All visual stimuli were rendered on a black background and back-projected onto a screen using the MR projector system installed at CUBRIC. The participant was asked to maintain central fixation.

5.2.3 Stimulus and Procedure

At the beginning, middle and end of each block, a white fixation cross was presented for 30 seconds. The recorded haemodynamic response during this time acted as a baseline. On each trial the participant was presented with a stimulus that they were to passively attend (S1) and a stimulus that they must respond to (S2), as illustrated in Figure 5.1. The first trial began immediately after the 30 seconds had lapsed. S1 was presented for 680ms and then followed by an ISI for 500ms. During the ISI, a grey fixation cross was presented; this was coloured grey to act as a cue to the participant that the following stimulus was the target stimulus to which they should respond. Following the ISI, S2 was presented for 680ms. The ITI were randomly jittered with a mean of 4s (ranging from 3s to 7s). Participants were asked to selectively attend to the feature of motion. A speeded response was collected within the presentation window of S2.

Participants completed a practice session the day before the experimental scanning session. The practice session was conducted in a darkened laboratory. Visual stimuli were presented at a mid-sagittal viewing distance of 50cm, on a 21 –inch CRT monitor

(60Hz vertical refresh rate; 1024/768 resolution; black background). Throughout the practice session, the participant's head was fixed within a chin rest. Although gaze was not monitored, the participants were asked to focus on the fixation cross at all times. Participants were given two practice blocks to complete; these were presented in the exact same way that they would be presented in the scanner. Therefore, there was an ITI jitter and a 30sec baseline at the beginning, middle and end. This was to ensure that the participant was familiar with the structure of the experiment to prevent confusion during the experimental session. After each of the 2 practice blocks, the RT and percentage of missed or anticipated responses (RT = <250ms) was calculated. If more that 10% had been missed, anticipated or answered incorrectly then they repeated that block. No participants were required to repeat the block during this experiment.

The stimulus consisted of 4 features: shape (circle or square), location (left or right), colour (red or green) and direction of motion (up or down). Depending on condition, these features could alternate or repeat between S1 and S2 independently of each other. The only feature that participants were asked to attend and respond to was the direction of motion. At the onset of S2, participants were required to press either a left (up) or right (down) button to decide whether the dots were moving up or down. This was counterbalanced across all participants. All participants were right handed and were asked to use their index finger on the left button and their middle finger to press the right button. S2 was only presented for 680ms and the participants were informed that only the first response was recorded and that once the S2 has disappeared, no responses were accepted.

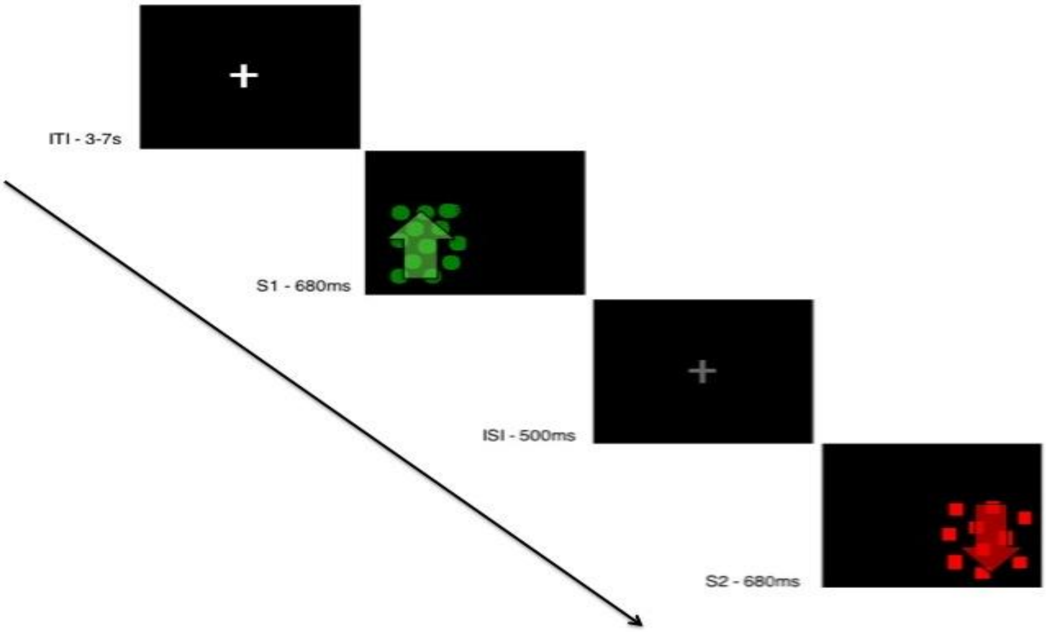


Figure 5.1. Schematic illustration of the displays and timings of events in a typical AC trial. The arrow denotes the direction of motion.

5.2.4 fMRI Data Acquisition

All data were acquired using a GE Signa HDx 3T scanner with an 8-channel head RF receive coil. T2*- weighted gradient echo fMRI data were acquired using an echo-planar imaging (EPI) pulse sequence with the following parameters; 53 interleaved oblique-axial slices (orientated along the participants AC-PC line) covering the whole brain, TR =3000ms, TE= 35ms, flip angle = 90 degrees, acquisition matrix= 64x64, slice thickness of 3.4mm, spacing between slice =3.4mm, parallel imaging acceleration (ASSET) factor 2. Each scanning sequence was comprised of 180 volumes and lasted for approximately 9 minutes. Participants completed 6 experimental runs. Each run consisted of 64 trials; 16 per condition. Structural scans were acquired using a T1-weighted fast, spoiled gradient recalled sequence (FSPGR) with the following parameters; 1mm isotropic resolution, acquisition matrix 256x256x176, TR/TE=7.9/3.0 ms, TI=450ms, flip angle=20deg. Fieldmaps were collected at the end of each scanning session. The fieldmap acquisition consisted of 2 SPGR scan with two different echo times of 7ms and 9ms. From these images, a phase-difference image was created to yield the frequency offset at each point in the fieldmap.

image pre-processing

The fMRI data were analysed using the FMRIB software library (FSL; www.fmrib.ox.ac.uk/fsl). Preprocessing parameters were as follows: motion correction using MCFLIRT (Jenkinson, Bannister, Brady & Smith, 2002); non-brain removal with BET (Smith, 2002). The fMRI data were then registered to the participant’s structural scan. All functional volumes were then smoothed with an 8 mm full-width half-maximum (FWHM) isotropic Gaussian kernel to compensate for residual between subject variations after spatial normalization. The resulting time series across each voxel were then high pass filtered to 1/128Hz.

Intra-subject analysis

5 event types were identified according to the 5 conditions: baseline (BL), NC, AC, RFC and IFC. Each event was separately modelled and lasted 1860ms from the onset of S1 to S2. 6 contrasts were calculated: IFC vs. NC, RFC vs. AC and each condition vs. BL

Statistical maps were generated using a fixed effects model. Both correct and incorrect responses were included in the analysis. Data was analysed by modelling the evoked hemodynamic response function (HRF) and its hemodynamic temporal derivatives (HRT) in the context of fixed effects general linear model. Contrasts of parameter estimates were then calculated to produce statistical maps for each contrast of interest. Each condition was contrasted with every other condition and each condition was contrasted with baseline. Baseline consisted of a white fixation cross. This was collected for 30s at the beginning, middle and end of each run.

Group level

The statistical maps then generated at the subject level were then entered into a group level mixed effects model. Voxel based thresholding was then applied to the resulting statistical maps (z=2.3), and cluster-based thresholding was used to correct for multiple comparisons, with a (corrected) cluster significance threshold of P=0.05.

2.2.5 Retinotopic Mapping Data Acquisition

Retinotopic mapping data were acquired using a gradient-echo EPI sequence with the following parameters; TR=3.0s, TE=35ms, Flip angle=90, 128x128 acquisition matrix, 256mmx256mm FOV, 37 2mm thick slices parallel to the calcarine sulcus, 100 volumes), spatial smoothing using a Gaussian kernel of full width half maximum (FWHM) 0.5mm. The stimuli consisted of 70 - degree wedges, rotating at 1 rpm, containing dots that moved and changed in a 3D flow pattern. In each session, two clockwise and two anti-clockwise runs were performed in a counterbalanced manner. Analysis of retinotopic data was performed using in-house software (developed by Krish Singh) that computed phase angle estimates with correction for hemodynamic lag for each voxels and estimated the strength of retinotopy, using the power of the variance in the time series at 1 rpm frequency. The phase angles were plotted as a coloured map on the flattened occipital cortex using mri3dX software, this is downloadable at: http://www.cubric.cf.ac.uk/Documentation/mri3dX.

Percent Signal Change analysis

Featquery was used to calculate percentage signal change in V5/MT during each condition (AC, NC, RFC, IFC). A mask of area V5/MT was created for each subject following retinotopic mapping and the percentage signal change each condition was calculated between the RFC and the AC condition and the IFC condition and the NC condition.

Once the percent signal change for each condition was calculated for each subject this was then entered into a 1X4 ANOVA in order to see if there was a significant change in BOLD signal during the RFC and IFC conditions over and above the AC and NC conditions.

Further to this we also carried out a correlation test in order to see whether there was a correlation between an individuals RFCC or IFCC and the percentage signal change in V5/MT.

In order to calculate the IFCC and the RFCC, I applied the same equations as explained in Chapter 3. These are repeated below for clarity.

Mean IFCC and RFCC for each subject

IFCC (ms) = mean RT of irrelevant feature change condition
- mean RT of no change condition

RFCC (ms) = mean RT of relevant feature change condition
- mean RT of all change condition

Mean percent signal change in V5/MT for each subject

IFCC (%) = mean % signal in V5/MT change during irrelevant feature change condition
- mean RT of no change condition

RFCC (%) = mean % signal change in V%/MT during relevant feature change condition
- mean RT of all change condition

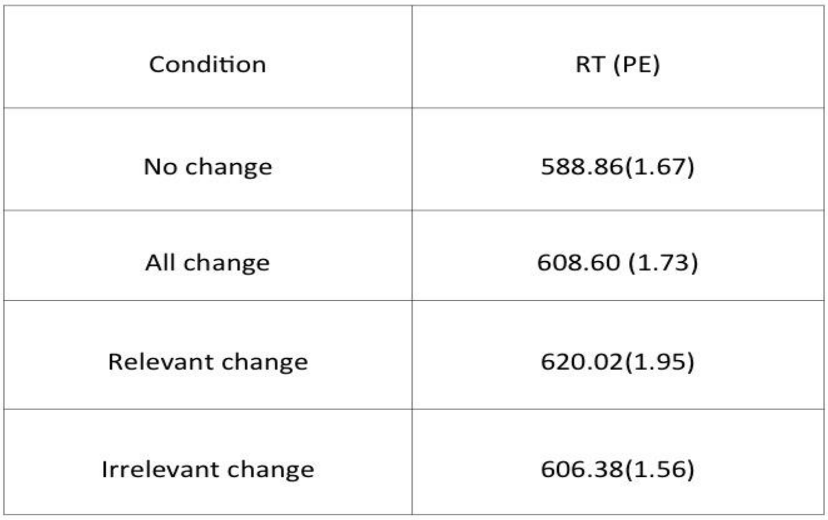
We then carried out a correlation test to see whether the mean percent signal change in V5/MT correlated with the mean RT cost during the RFCC and the IFCC at the individual level.

5.3 Results

5.3.1 Behavioural results

Responses were missing or anticipated (<250ms) in 1.4% and 0.4% of the trials, respectively. Trials with missing or anticipated responses were excluded from analysis. For the remaining data, mean RTs and PEs were calculated for each experiment as a function of the 4 possible relationships between S1 and S2; that is, whether all features repeated or alternated, or whether only the attended or unattended feature alternated (Table 1). A 1x4 ANOVA with repeated measures was carried out to analyse the results. A 1x4 ANOVA revealed that there was a main effect of condition on RT (F (3,2.215)=17.164, <0.001), partial η^2 = 0.47), therefore replicating results from experiment 3 and previous studies (Hommel, 1998, 2004; Keizer et al. 2008).

Table 5.1. Mean RT Across All Participants in Each Condition



Condition	RT (PE)
No change	588.86(1.67)
All change	608.60 (1.73)
Relevant change	620.02(1.95)
Irrelevant change	606.38(1.56)

Note. **The PE is displayed within the brackets. RT = reaction time; PE = percentage error.**

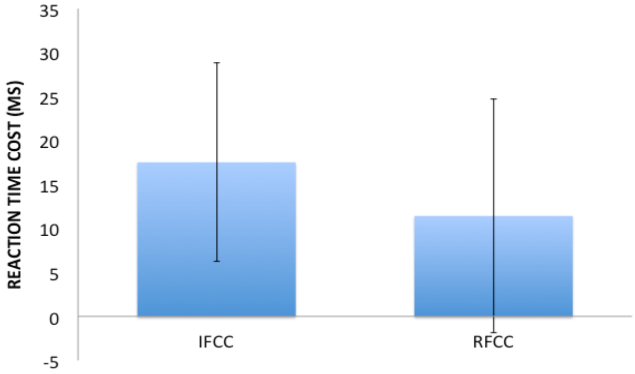


Figure 5.2. RT Benefit and Costs. The IFCC bar represents the increase in RT observed when an irrelevant feature (colour, shape or location) alternated between S1 and S2 (contrasted to when no features changed). The RFCC bar represents the increase in RT observed when a relevant feature alternated between S1 and S2 (contrasted to the all change condition) RT = reaction time; IFCC = (IFC-NC) ; RFCC= (RFC – AC), OSB = (NC-IFC). Error bars=SEM.

The IFCC was calculated by subtracting the mean RT during the NCs (606.38ms) from the RT in the IFCC (588.86ms) and the RFCC was calculated by subtracting the mean RT during the ACs (608.2ms) from the RT in the RFC (620.02ms). The 1x4 ANOVA showed that there was a significant increase of RT when a task irrelevant feature was changed between the presentation of S1 and S2, in comparison to when no features changed (mean difference =18ms, P=0.009, partial η^2 = 0.0422). The 1x4 ANOVA showed that there was a significant increase of RT when the task relevant feature was changed between the presentation S1 and S2, in comparison to when all features changed (mean difference =11ms, P=0.011, partial η^2 = 0.406). I do not report the OSB here as this is simply the reverse of the IFCC.

5.3.2 Errors

A 1x4 ANOVA was carried out on the percentage of errors across conditions. The mean percentages of errors (PE's) are displayed in table 1. The ANOVA revealed no significant main effect of condition on error rate, (F(3,57)=0.103,P=0.958, partial η^2 =0.005.

5.3.3 Imaging Results

This experiment calculated 2 fMRI contrasts in order to reflect the same behavioural contrast as above. This also enabled the differentiation between the cortical pathways engaged in a RFC (Figure 5.3) and an IFC (Figure 5.4). Further to this, the two contrasts also allowed us to match the motor switch or repetition effects between conditions.

Table 5.2 The brain areas that showed increased levels of BOLD are presented along with the MNI co-ordinates of the peak voxel within the cluster.

Contrast	Brain Areas	X	Y	Z	Max Z score	P	No. of voxels
IFC-NC	R Lateral Occipital Cortex	30	-80	18	3.64	0.0363	468
	R Occipital Fusiform Gyrus	26	-72	-12	4.25	0.0205	522
	L Superior Frontal Gyrus	-28	-6	56	3.83	0.0081	613
	L Lateral Occipital Cortex	-20	-74	26	3.75	0.0035	699
RFC-AC	L Postcentral Gyrus	-46	-24	52	4.99	<0.001	2041
	R Lateral Occipital Cortex	14	-96	2	17.4	<0.001	4058

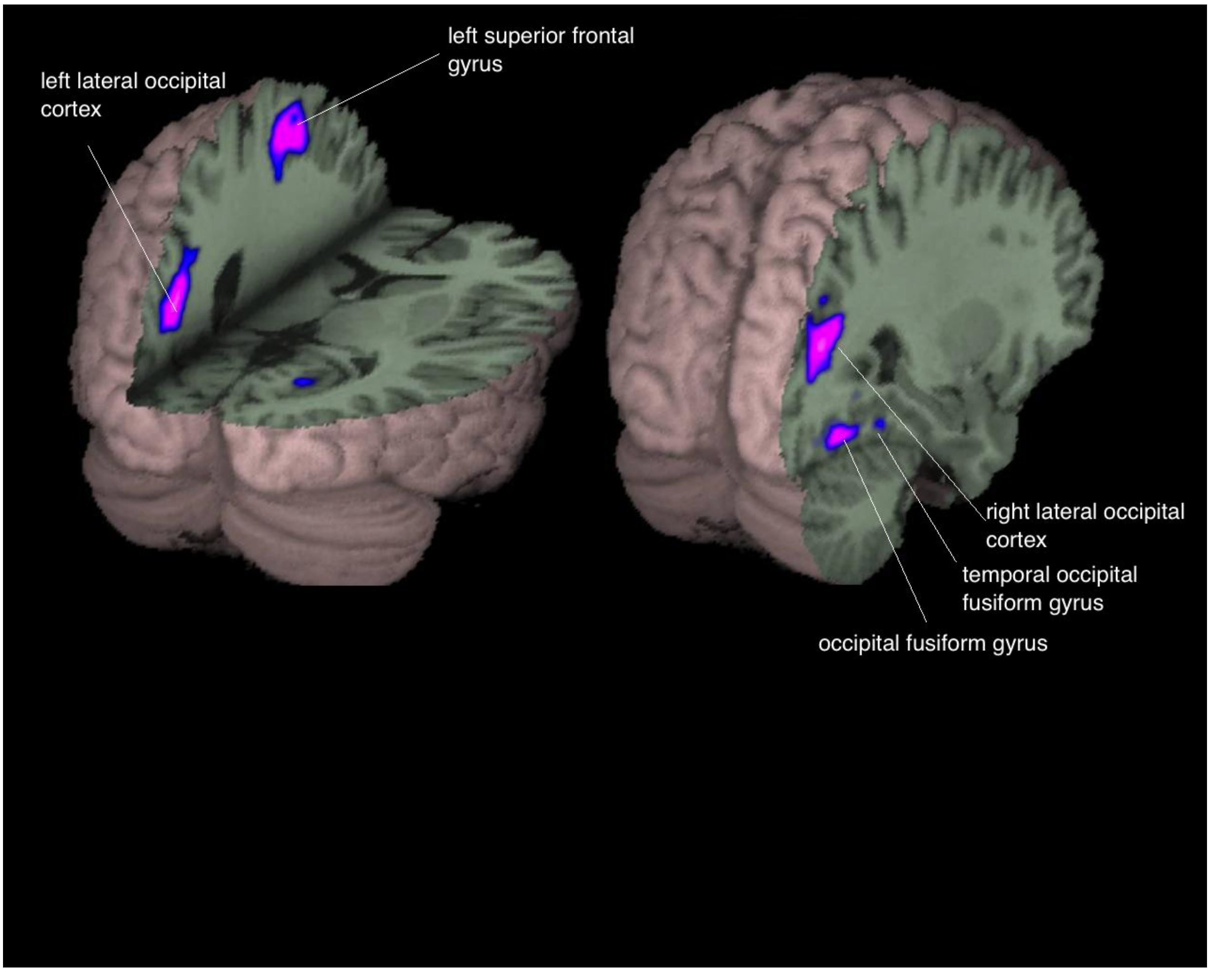


Figure 5.3. The cortical areas that showed increased levels of BOLD when a irrelevant feature alternated between S1 and S2, as opposed to trials where all features repeated (IFC Vs NC).

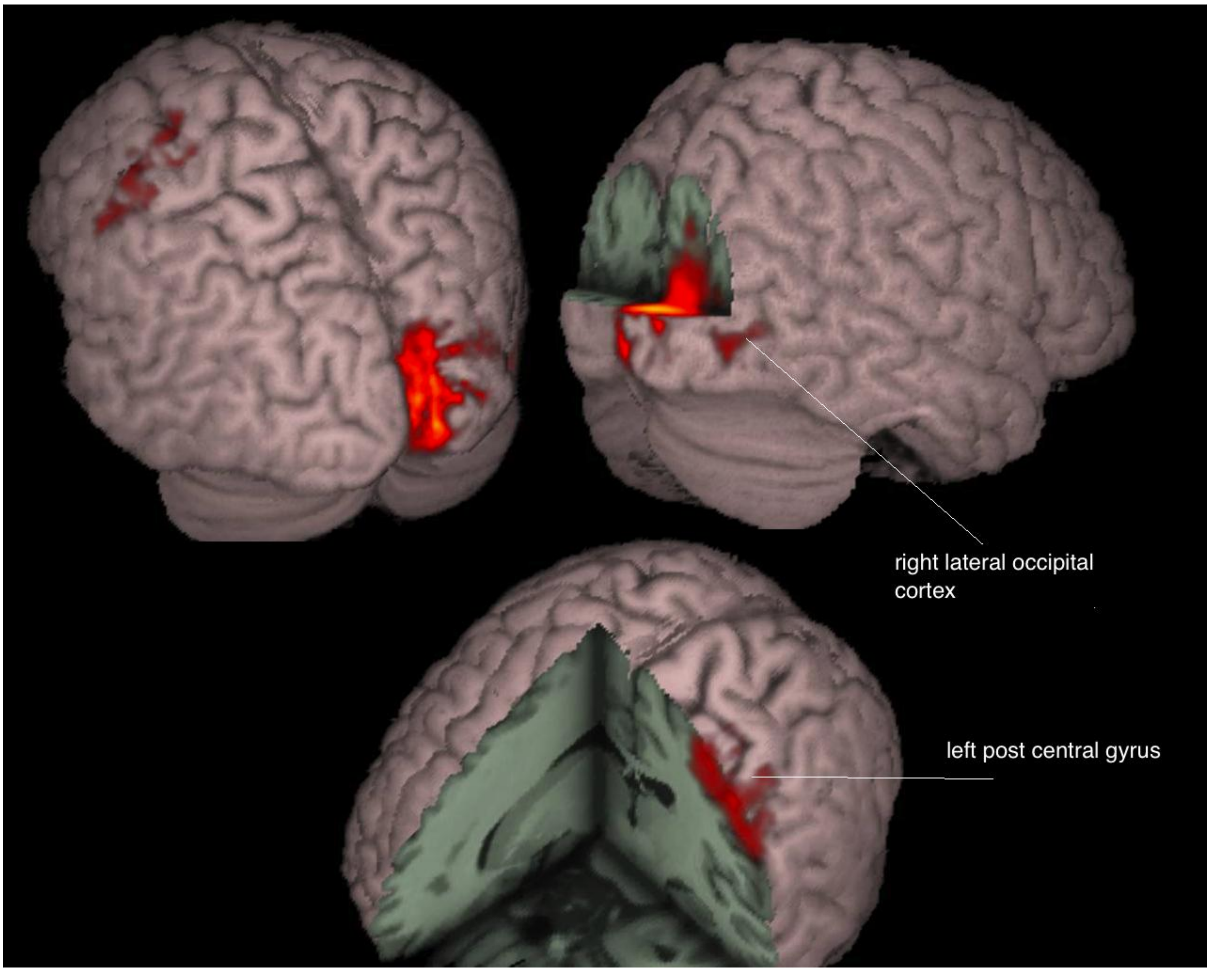


Figure 5.4. The cortical areas that showed increased levels of BOLD when a relevant feature alternated between S1 and S2 as opposed to trials where all features alternated (RFC Vs AC).

5.3.4 ROI Analysis and Percent Signal Change in MT: Brain-Behaviour Correlation

A ROI analysis was carried out on area MT. Area MT was chosen because it is a specialised processing area for motion, which was the task relevant feature. If alternating one task feature led to an increase in RT, in contrast to either repeating or alternating all features, it was hypothesised that the theoretical rebinding that drives the RT cost would be associated with an increase in BOLD in area MT. A 1X4 ANOVA was carried out to look at whether a significant difference in BOLD signal was present in conditions that carried the RT cost. The method of this calculation is explained on page 120. Only the relevant change condition showed a significant increase in BOLD above and beyond that of the IFC condition. No other condition significantly differed from any other. The results are displayed in the table 5.2 below.

Further to this we tested whether there was any correlation between an individual's IFCC and RFCC and their individual increase in BOLD in MT. A positive correlation was expected between the percentage signal change in MT and the RT cost observed, as found in previous experiments (Keizer et al. 2008). A percentage signal change was calculated separately for both IFCC and RFCC to control for the confounding impact of the motor repetition effect previously explained. Percentage signal change difference was calculated as per explained in the methods section.

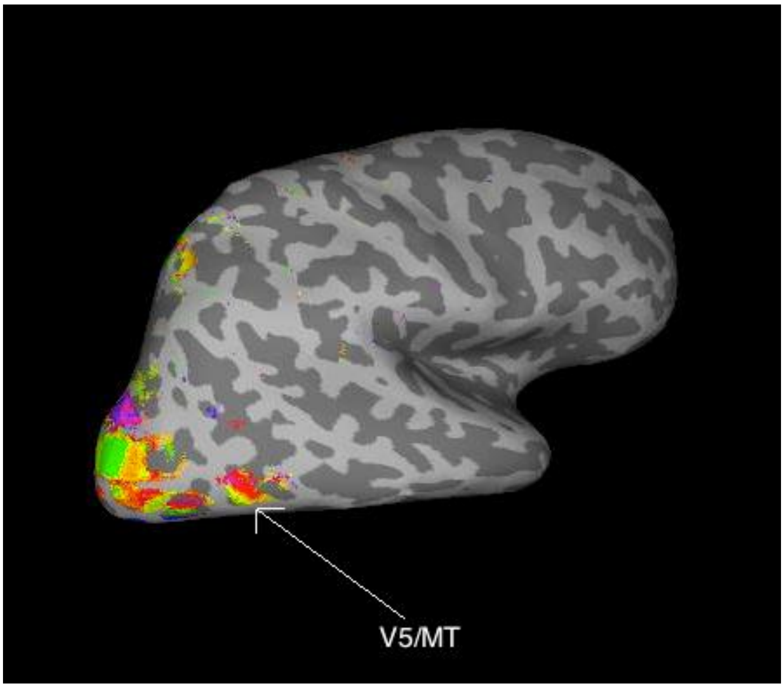


Figure 5.5 shows an example of a retinotopic map and area V5/MT. Once this area was defined then a mask was created. This mask was then used in featquery to extract the percent signal changes in this area of the cortex.

Table 5.2 ROI Analysis Results: Mean percentage change in BOLD signal within area MT in the contrasts specified.

(A) S1S2 RELATIONSHIP	(B) S1S2 RELATIONSHIP	MEAN DIFFERENCE (B-A)	STD. ERROR	SIG
NO CHANGE	ALL CHANGE	-0.066	0.05	>0.99
	RELEVANT CHANGE	-0.05	0.054	>0.99
	IRRELEVANT CHANGE	-0.105	0.053	0.367
ALL CHANGE	NO CHANGE	0.066	0.05	>0.99
	RELEVANT CHANGE	0.017	0.017	>0.99
	IRRELEVANT CHANGE	-0.039	0.022	0.59
RELEVANT CHANGE	NO CHANGE	0.05	0.054	>0.99
	ALL CHANGE	-0.017	0.017	>0.99
	IRRELEVANT CHANGE	-0.056*	0.018	0.032
IRRELEVANT CHANGE	NO CHANGE	0.105	0.053	0.367
	ALL CHANGE	0.039	0.022	0.59
	RELEVANT CHANGE	0.056*	0.018	0.032

These predictions were not confirmed. Participants did not display the predicted positive correlation for IFCC (Figure 5.6) or RFCC (Figure 5.5): the RT cost associated with alternating either an irrelevant or relevant feature was not significantly correlated with an increase in BOLD in the relevant features processing hub (MT).

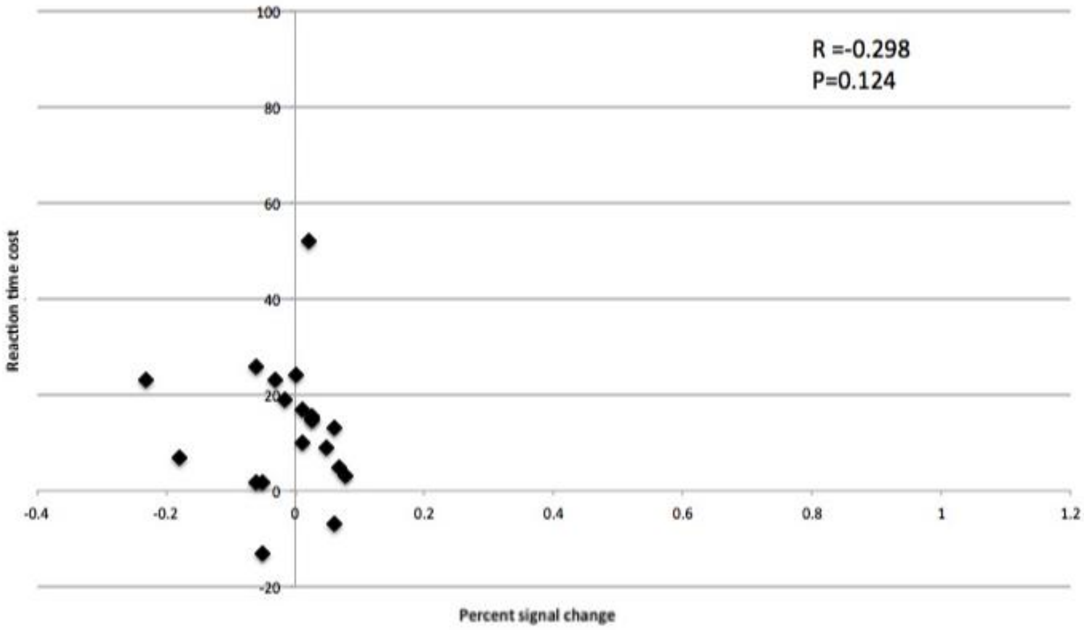


Figure 5.6. Correlation between the RFCC in reaction time and the percentage BOLD change in the RFC >AC conditions in area V5/MT. The difference between the percentage signal change in the RFC condition and the AC was calculated. This was then plotted against the RFCC which was calculated by subtracting the RT in the RFC condition from the RT during the AC condition. There was not a correlation between the increase in RT observed in the RFC and the percentage increase in area MT. RFC = relevant feature change; AC = all change; RT = reaction time; MT = medial temporal.

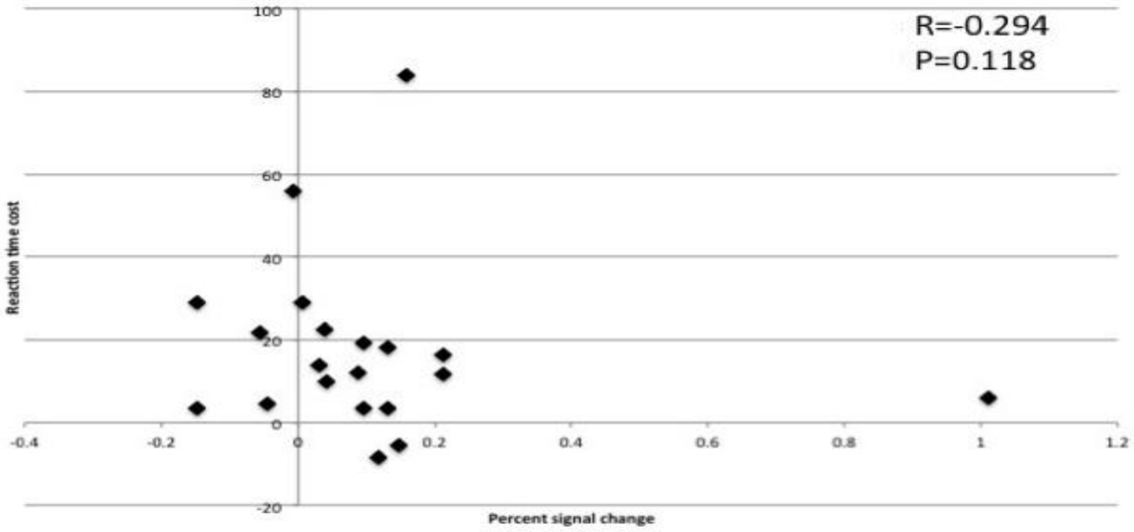


Figure 5.7. Correlation between the IFCC in reaction time and the percentage BOLD change in the IFC >NC conditions in area V5/MT. The difference between the percentage signal change in the IFC condition and the NC was calculated. The IFCC was then calculated by subtracting the RT in the NC condition from the RT in the IFC condition. This was then plotted against the difference in relation to RT in the IFC condition and the NC.

5.4 Discussion

The aim of this study was to explore cortical areas that were engaged during partial repetition trials, in which a RT cost is often observed. We also aimed to determine whether a task RFC would engage a different cortical network than a task IFC. Alongside a whole brain analysis, a ROI analysis was carried out on area MT to establish whether we would see an increase of BOLD in this area that would correlate with the partial repetition cost observed behaviourally. We also looked at whether the individuals IFCC and RFCC correlated with the BOLD signal in area MT on a subject level. The behavioural results replicated previous findings (Hommel, 2004; Hommel, 2008) was replicated and a significant increase in RT was observed when either a task relevant or irrelevant feature was alternated relative to the AC and the NC, respectively. The whole brain analysis revealed that the cortical pathway engaged during a task RFC was different from the cortical areas engaged during an IFC. A RFC led to 2 large and significant clusters of activity in the right LOC and the left PCG, whereas a task IFC led to both the left and right LOC becoming engaged alongside the SFG and the MFG.

In the ROI analysis we saw a significant increase in BOLD during the RFC condition in contrast to the IFC condition. A key difference between the RFC condition and the IFC condition is the latter involved the repetition of a direction of motion between S1 and S2. The repetition of features as opposed to the presentation of new features may have led to an attenuation of the BOLD signal. Both the IFC and NC task both encompass a repetition of the direction of motion; this may have led to adaptation of the BOLD signal in the motion sensitive areas such as V5/MT, whereas the RFC and AC conditions involved an alternation between two motion directions and would lead to a relative increase in the BOLD signal. The data supports this hypothesis, RFC led to a significant increase in BOLD (0.056%) in area V5/MT in contrast to the percentage change in BOLD during the IFC condition.

Since there is no published fMRI that has carried out a whole brain analysis using the reviewing paradigm, this experiment can be classified as exploratory and therefore, that should be considered while interpreting the results. The RFC trial consisted of the direction of motion changing between S1 and S2 while the location, shape and colour feature were repeated. This condition was contrasted to the AC where the location, motion, shape and colour feature alternated. The largest cluster seen in response to the RFC was in the left PCG. Since both conditions are matched in terms of motor actions and motor switch costs, this result was unexpected. An explanation for this cluster of activity could be found in the previously discussed data, which establishes that object files contain more than just perceptual information.

Hommel (2004) has shown that the motor action afforded by that object also becomes bound alongside the features of the object. Therefore, if the RFC caused the retrieval or reactivation of the object representation formed in S1, then it may be possible that the motor action afforded by the previously presented direction of motion is being retrieved and overwritten alongside the RFC. The somatosensory cortex has been shown to play an important role in the formation of goal directed actions, and therefore the retrieval of a primed but not actioned movement may have led to an increase of BOLD in the post central gyrus. Due to the RFC condition being contrasted to the AC, the motor switch cost would have been controlled. However, one could argue that the perceptual overlap in the RFC condition would have led to the reactivation of the previous object, and hence the attached motor action. There is no perceptual overlap between S1 and S2 during the AC condition, therefore, theoretically, would not have led to a reactivation of the previous motor action. A further explanation for the increase of BOLD in the left PCG during the RFC condition is the accompanying increase of RT during the RFC conditions. Although RT is one of the most widely used measures of performance in experimental psychology, relatively few fMRI studies have explored the neural correlates of RT variability (Yarkoni et al. 2009). Previous experiments have shown an increase in the power of BOLD in correlation with an increased RT (Honey, Bullmore & Sharma, 2000). Therefore, this could explain an increase of BOLD in the motor region if the RFC was causing an increase in RT, caused by response conflict by reactivating S1. The second significant cluster of activity was in the right LOC. The LOC is a cortical area that shows preferential processing for objects (Kanwisher, Chun, McDermott & Ledden, 1996).

To identify areas engaged during an IFC trial, the IFC condition was contrasted to the NC condition. There were 2 main clusters of activity observed: bilateral LOC and the left SFG; as well as spreading over the right MFG. The frontal cluster observed that was covering both the left MFG and SFG indicated that a task irrelevant alternation is leading to perceptual conflict. Activity in these areas have been associated with the ability to inhibit responses (Swick, 2011; Muggleton, Chen, Tzeng, Hung and Juan, 2010) and in particular the SFG is thought it contribute to higher cognitive functions, particularly working memory (Boisgueheneuc et al. 2006). It is thought that the highest level of executive processing and spatial orientated processing triggers the participation of this region. Within the working memory, the SFG is specifically thought to be integral to the monitoring and manipulating of information (du Boisgueheneuc et al. 2006). This suggests that irrelevant features are integrated spontaneously and the alternation of a task irrelevant feature leads to a retrieval of the previous representation and an update within working memory. This is contrary to what is suggested by Xu et al. (2010), where irrelevant features are shown to be processed to a lower level and degrade much quicker than other features.

In order to determine when object-based processing may or may not occur, Xu et al, (2010) varied the overall task encoding load and measured the processing of object shapes when attention was directed to object colours. In essence, the processing of an irrelevant feature was examined by measuring fMRI responses in the LOC, an area of the brain involved in object shape representation. In three experiments it was found that, whereas object based processing was present at low colour encoding load, it was attenuated or even suppressed at high colour encoding load. The authors found that even when task irrelevant shapes were encoded by the LOC, this information was not processed and retained in the superior IPS, a brain area involved in VSTM information encoding and storage (Todd & Marois, 2004; Xu & Chun, 2006).

In the current experiment the encoding load of the task relevant feature is relatively low; participants have one object to focus on and must decide whether the direction of motion is up or down, therefore in the context of Xu et al. (2010) results it is unsurprising that we see bilateral activation of the LOC and SPL suggesting that during this task object based processing is taking place and irrelevant features are being processed to a higher level. However, unlike Xu et al. (2010) study, there is not just two features being manipulated; an IFC trial can be either a shape colour or location change. Due to the role of the left SFG in spatial orienting, we do not know whether the spatial alternation is driving the BOLD cluster, or whether this area is involved in resolving the perceptual conflict. In order to gain insight into the causal role in the formation of object files within these areas, it is necessary to apply TMS to these areas. In the following chapter, continuous cTBS is used to inhibit the left PCG, right SFG and right LOC.

Chapter 6 – Experiment 5

Using cTBS to probe the cortical network of feature binding

6.1 Introduction

The final experiment in this thesis aimed to demonstrate the causal roles of the areas identified in the whole brain analysis carried out in experiment 4. This is the first documented TMS study using the *reviewing paradigm*. We applied an offline protocol of continuous theta-burst stimulation (cTBS; see Huang et al. 2005) to 3 cortical sites: namely the right LOC, left SFG and the left PCG. Results indicated that cTBS to the left PCG led to significant decrease in RT in comparison to the sham condition but only in the AC condition. This was also true of the right LOC. However TMS to the left SFG did lead to a significant decrease in RT during the irrelevant change condition. This is important, as this was an area that showed a significant increase in activity during the completion of the task, as shown in experiment 4. As this is the first time the reviewing paradigm has been explored using cTBS these results are preliminary and hence should be interpreted with caution. This chapter begins with a brief introduction to TMS.

6.1.1 Background

Transcranial magnetic stimulation (TMS) exploits Faraday's principle of electromagnetic induction. Passing a powerful and rapidly changing current through a wire produces a magnetic field. When this wire is within a coil and the coil is placed against the scalp the magnetic field passes through the cranium, virtually unimpeded and relatively painlessly to the cortical tissue below. An eddy current is then induced in the cortical tissue, and this in turn penetrates the membranes of the neurons. This results in either an action potential or an excitatory or inhibitory post-synaptic potential (Terao &Ugawa,2002).

The first studies of transcranial magnetic stimulation (TMS) were performed in 1985 and demonstrated that TMS of the motor cortex could safely produce observable movement of the hand (Barker, Jalinous & Freeston, 1985). Although early studies were based around the application of single pulses of TMS, research quickly expanded and TMS developed to allow the administration of multiple pulses over a short period of time. This was termed repetitive transcranial magnetic stimulation (rTMS). rTMS was shown to have lasting effects on cortical excitability that persisted after the actual delivery of the rTMS had ceased (Chen et al. 1997).

When TMS is applied at appropriate intensities, the induced electrical current is sufficient to depolarize neurons and create action potentials (Pascual-Leone et al. 2002). Although single pulses do not carry effects that last longer than a few seconds, when pulses are applied in a repetitive manner with a short inter-stimulus duration (typically 1Hz or greater) the effects outlast the time of stimulation by up to 60 minutes (Siebner & Rothwell, 2003).

A relatively recent development has seen the introduction of a novel rTMS protocol (Huang et al. 2005) termed theta burst stimulation (TBS). During TBS, pulses are applied in triplets delivered at a frequency of 50Hz and an inter-burst interval of 200ms, resulting in an envelope frequency of 5Hz (theta band). TBS was developed following the observation that theta rhythms as measured by EEG were associated with long-term potentiation. It has been observed that TBS protocols appear to lead to sustained changes in cortical activity lasting well beyond the duration of the TMS application (Oberman, Edwards, Eldaief and Pascual Leone, 2011).

There are two main types of TBS, continuous TBS (cTBS) and intermittent TBS (iTBS). It has been shown that cTBS reduces the motor evoked potential (MEP) whereas iTBS increase the MEP suggesting an inhibitory and excitatory effect, respectively (Cárdinas - Morales, Nowak, Kammer, Wolf and Lecuona, 2010).

Experiment 5 employed cTBS in an attempt to selectively inhibit specific cortical areas in order to further assess the causal role that they play in the formation of object representations. By inhibiting areas that have shown an increase in BOLD activity during specific conditions of the reviewing paradigm I aimed to selectively interfere with the reaction time observed during the reviewing paradigm.

Previous literature (Xu, 2010) and results from experiment 4 have shown that task irrelevant features seem to have separate cortical and perceptual fate, meaning that the irrelevant features not only play a different role in the binding process but also, when processing an irrelevant feature change (IFC) between two objects, recruit a different cortical pathway that of an relevant feature change between two objects (RFC). Further to this it has been shown that not all features are of equal salience in the visual processing of objects; that is, features such as location seem to have higher salience than colour (Chen, 2009). Although it has been shown that a task irrelevant feature modulates processing of the whole object, it has been argued that task irrelevant features degrade more rapidly and are processed to a much lower degree (Xu, 2010).

Spatial attention has a heavily documented role in visual feature binding (Tresiman et al. 1984) and, alongside this, it is established that the parietal cortex is recruited during the engagement of spatial attention (Corbetta et al. 2008). This is one of the key reasons why the parietal cortex has been an area of interest when applying rTMS as a method of probing the cortical substrate of feature binding. Esterman et al. (2007) applied offline 1Hz rTMS to the right IPS, right AG/TOS and the left IPS. Only TMS to the right IPS led to a decrease in illusory conjunctions, which suggests an improvement of accurate feature binding.

Further to this, Esterman, Verstynen and Robertson (2006) applied TMS to the posterior parietal lobe. The participants who completed the feature binding task were deemed colour – grapheme synesthetes. Colour-grapheme synaesthesia is a condition in which graphemes are automatically bound with colours. For example, the letter “A” is always perceived in a particular shade of blue. Synaesthesia is thought to be an example of hyper-binding that may rely on similar mechanisms to normal perceptual feature binding (Cohen-Kadosh & Henik, 2006; Robertson, 2003; Sagiv, Heer, & Robertson, 2006). Results showed that in contrast to sham, rTMS of the right parietal ROI decreased reactions times (RT), so that subjects became faster, on trials where the stimulus colour and synesthetic percept were incongruent. The authors suggest this is because the interference between features has been attenuated following rTMS to the right parietal lobe.

The parietal lobe has received a lot of focus, which has been at the neglect of other cortical areas that may play a key role in visual feature binding. Visual feature binding is a deceptively complex process that engages a widespread neural network due to integration of perceptual, motor and behavioural goals. These fundamental processes include the short-term maintenance of relevant information, the mental manipulation of this information and the mental organization of the forthcoming sequences of actions (Baddeley, 1996; Goldman-Rakic, 1987, 1995). Boisgueheneuc et al. (2006) reported that the left SFG, in particular, showed a significant increase in BOLD during tasks that engaged these fundamental processes. Their results suggest that the left SFG is highly involved in processes gathered under the concept of 'monitoring and manipulation' (Duncan &Owen, 2000) or 'executive processing' (Postle et al. 2000) within WM. Boisgueheneuc (2006) asserts that the left SFG is recruited by the specific task that includes the maintenance of two or three items in short term memory. During the preview task it is thought that the RT modulation is observed because the features of an object become automatically bound and are present in visual working memory for up to 4 seconds (Hommel & Colzato, 2004), this representation is then updated and/or maintained if certain conditions are met. The selective activation of this area observed during an IFC condition suggests that on viewing S2 there is a manipulation of information being held in the working memory. Therefore the left SFG may play a key role in process of feature binding. During experiment 4 we saw an increase of BOLD in the left SFG during the irrelevant feature change task when contrasted to a no change task. The irrelevant feature change involves manipulation of the current representation to incorporate the new information. This is not necessary during a no-change condition as all the information is repeated.

The aim of experiment 5 was to selectively inhibit the left SFG. As the SFG showed increased activity during the IFC condition in experiment 4, it would be expected that inhibition of this area would lead to an inhibition of the manipulation of information and therefore an increase in RT and/or errors during the IFC condition, while leaving the NC and AC condition unchanged in contrast to the RT observed following sham cTBS.

The second site of stimulation in this experiment was the right LOC. During experiment 4, the LOC has shown an increase in BOLD during in both the RFC condition and the IFC condition. As both the RFC and IFC conditions are thought to evoke the binding process due to the partial overlap of features, the right LOC is a likely candidate as a key cortical substrate in the process of rebinding. If the recruitment of the right LOC is purely due to the rebinding or updating of the current object representation then we would expect an inhibitory protocol cTBS to the right LOC to lead to increased RT and/or error rates in the RFC and IFC conditions only. However, if the right LOC plays a general role in processing all stimuli presented then we should see a general increase in RT across all four conditions, in contrast to the sham condition.

The third site of cortical stimulation is the left somatosensory cortex or the left PCG. The large cluster observed in the left PCG in response to a RFC over and above an AC condition was unexpected. Both conditions were matched in motor demands and both conditions would have incurred a motor switch cost. The somatosensory cortex lies within the anterior parietal cortex, posterior to the central sulcus, and is characterised by its map of sensory space called the sensory homunculus. Following damage to this area patients often have difficulty identifying an object by active touch of the hands without other sensory input (Valens, 2001).

The relevant feature motion carries with it an associated task response. In both the AC and RFC conditions the direction of motion presented in S1 (up or down) is alternated so that the direction of motion in S2 is opposite to that in S1. This means that the motion direction in S1, although irrelevant, has primed the participant to a button press. When the direction of motion changes on the presentation of S2 there is a then a motor switch cost invoked. As the motor switch is constant across the two conditions, the main difference in these conditions is that the RFC condition would have involved the manipulation of one feature, therefore updating an object; whereas the AC condition would have no interaction with the previously presented object in S1. This may have prevented the action from S1 being processed as a prime. Turella, Tubaldi, Erb, Grodd and Castiello (2012) investigated the influence that the presence of an object, intended as the target for action, might have on the action observation network (AON). This network includes both the motor and somatosensory cortices. This suggests that viewing an object automatically entails processing the action that the object affords. Hommel (2004) has shown that object files do not just contain information regarding perceptual features but also contain information regarding actions. Therefore an explanation for this cluster of activity may lie in the over-writing or manipulation of the goal oriented motor action that the three features repeated from S1 may have re-activated. If this is the case then applying inhibitory cTBS to the left PCG may lead to a slower RT in the RFC condition in contrast to the AC condition in contrast to those observed following sham cTBS.

In summary by applying cTBS to the selected areas that were recruited in response to the RFC and IFC conditions, this preliminary experiment seeks to address the causal role of these areas in the rebinding and updating of an object representation in both the RFC and IFC condition.

6.3 Method and Materials

6.3.1 Participants

10 participants undertook experiment 5, for which they were reimbursed £10 per hour (mean age 23, SD = 2.5 years; 6 females). Three of the participants also took part in experiment 4. All provided informed consent and were screened for contraindications to TMS, including personal or family history of epilepsy (Maizey et al. 2013). This research was approved by the Ethics Committee, at Cardiff University School of Psychology.

6.3.2 Stimulus and Procedure

The stimulus was displayed on a 21-inch CRT monitor (vertical refresh rate of 60Hz; 1024/768 resolution; black background) with a mid-sagittal viewing distance of 50cm. Participants were asked to place their head in the chin rest and maintain focus towards the centre of the screen. Eye movements were not measured. During the trials, participants responded by pressing either a left button or a right button on the number keypad on a keyboard centred in front of them.

The paradigm was identical to the stimulus used in experiment 4 with the only exception being the removal of the inter-trial jitter. Instead, the ITI was adjusted to a constant 2000ms. Prior to the 4 main experimental sessions each subject completed approximately 2-3 hours of preparatory testing. During this phase participants were screened for suitability for TMS, and the motor threshold was obtained (Varnava, Stokes and Chambers, 2011). Participants then completed 4 individual sessions that lasted up to 1 hour each consisting of 6 blocks of 64 randomised trials, consisting of the 4 conditions of S1 and S2 combination in a randomised order. There were 3 active TMS sessions and a sham session to provide a baseline.

The sham TMS session consisted of the TMS coil being held at 90 degrees to the scalp. The order of sessions was balanced in a Latin square design. Eight minutes was allocated for each block: as each block lasted around 6 minutes, a short rest period was included. The first experimental block started within 30 seconds of the cTBS ending meaning that data were collected up to 40 minutes after the cTBS had started.

5.3.3 Equipment and TMS Procedure

Cortical stimulation was delivered with a Magstim figure-8 coil in conjunction with a Magstim Rapid2 biphasic stimulator. A standard continuous theta-burst stimulation (cTBS) protocol was applied (burst of 3 pulses in 50Hz, repeated at 5Hz; 200 bursts over 40s, 80% of individual resting motor threshold). Motor threshold was established using the observation of movement method and was calculated as the average across the hemispheres (Stokes et al. 2005;Varnava, Stokes & Chambers, 2011). Positioning was achieved using a miniBIRD system (Ascension Technology Corp) in conjunction with the MRIcro and MRI reg software (Chris Rorden) and structural MRI scans (Rorden & Brett, 2000). TMS was targeted at 3 main sites that were chosen based on the MRI co-ordinates of significant clusters of activity in experiment 4. Theses 3 areas and MNI co-ordinates were as follows: right LOC (14 -96 2), Left SFG (-24 4 58) and the left PCG (-46 -24 52). In order to use the MNI coordinates as a TMS site, the co-ordinates from the fMRI data were converted into individual non-normalised x-y-z space using SPM5. The TMS coil was oriented ~45° laterally from the midline with the handle pointing caudally.

6.4 Results

Reported p values were adjusted for violations of sphericity using the Greenhouse-Geisser correction. A 4X4 (TMS site X S1-S2 condition) repeated-measures ANOVA was carried out on the reaction time data from correct trials. This revealed a significant main effect of TMS site, F (3,27)= 11.07, P= <0.001, η_p^2 = 0.570. There was also a main effect of condition, F (3,27) =9.206, P<0.001, η_p^2 =0.506.

There was also a significant interaction between the TMS site targeted and the S1- S2 relationship, F (9,81)= 6.980, P<0.001, η_p^2 = 0.437. These results are explored in more depth below.

6.4.1 Error data

A 4x4 ANOVA was carried out the percentage of error made in each experimental condition after each TMS session (TMS site X S1-S2 condition). The dependent variable was the percentage of errors from each subject in each condition following sham, left SFG, left PCG or right LOC cTBS. The results showed that there was no main effect of S1 –S2 condition on the observed error levels across the 4 conditions of AC, NC, RFC and IFC, F(3,27)=1.008, P=0.405, η_p^2 = 0.101. There was also no significant main effect of TMS site, F(3.27)= 0.565, P=0.643, η_p^2 =0.059. There was also no significant interaction, F(9,81)= 0.900, P=0.530, η_p^2 = 0.091

6.4.2 TMS Site

There was a main effect of TMS site F(3,27) =11.907, P=<0.001, η_p^2=0.570, with TMS being applied to the left SFG resulting in a slower RT than both the application of TMS to the right LOC (Mean difference = 31.62ms, P=0.003) and the left PCG (Mean difference =35.275ms, P=0.002).

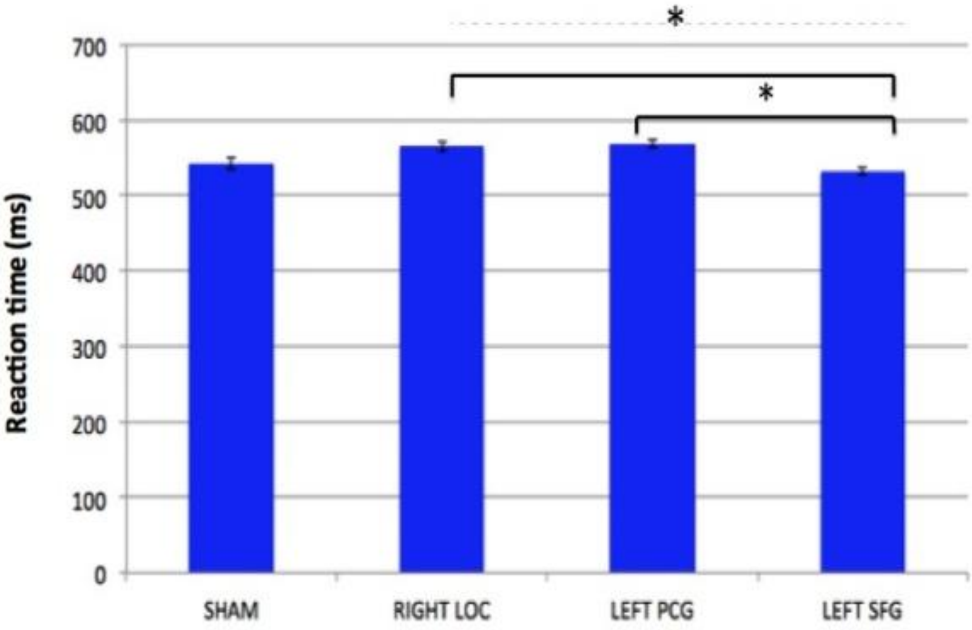


Figure 6.1. TMS Site. There was a main effect of TMS site with TMS being applied to the left SFG resulting in a faster RT than both the application of TMS to the right LOC and the left PCG (31.62ms and 35.27ms respectively). Error bars = SEM. The * denotes the sites of stimulation that led to a significant change in RT in contrast to the sham condition.

6.4.3 S1-S2 Relationship

There was also a significant effect of S1-S2 relationship condition, F(3,27)=9.206, P=<0.001, η_p^2= 0.506. Overall, participants were significantly slower responding to the RFC condition (601 msec) than the AC condition (520.20 msec) and the NC condition (519.20msec), P<0.001. However, there were no other significant differences between conditions.

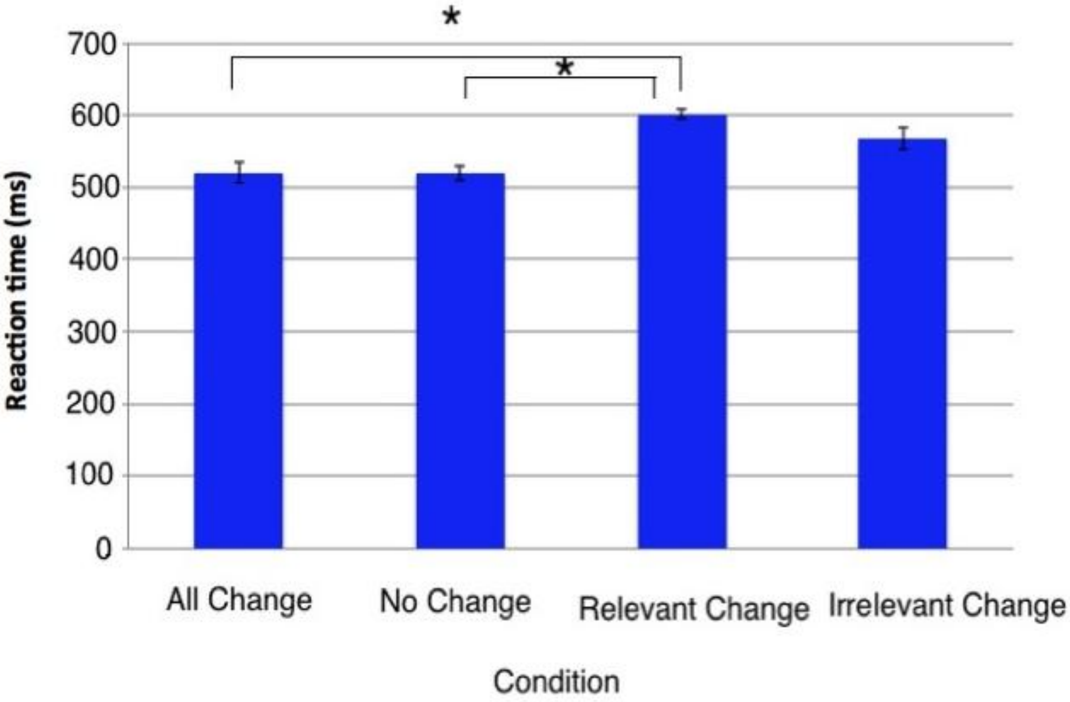


Figure 6.2. The mean RT plotted as a function of the S1-S2 Relationship across all experimental conditions. Error bars = SEM. The * denotes the sites of stimulation that led to a significant change in RT in contrast to the sham condition.

6.4.4 TMS site x S1-S2 relationship

As noted above, there was also a significant interaction between the site that received cTBS and the AC, NC RFC and IFC conditions, F (9,81)= 6.980, P= <0.001, $\eta_p{}^2 = 0.437$. To explore this further I carried out four 1X4 ANOVAs (site x condition).

All change

The all change condition does not lead to a reactivation of a previous representation and therefore does not lead to a reaction time cost. The reaction time observed during this condition represents the time it takes to form a new representation. There was a significant main effect of TMS across the AC conditions, F(3,27)=5.707, P=0.004, $\eta_p{}^2=0.388$. Following cTBS to the right LOC and left PCG there was significant increase in RT (MD=42.1ms,P=0.018, $\eta_p{}^2=0.642$; MD=86.7ms, P=<0.001, $\eta_p{}^2 = 0.550$).

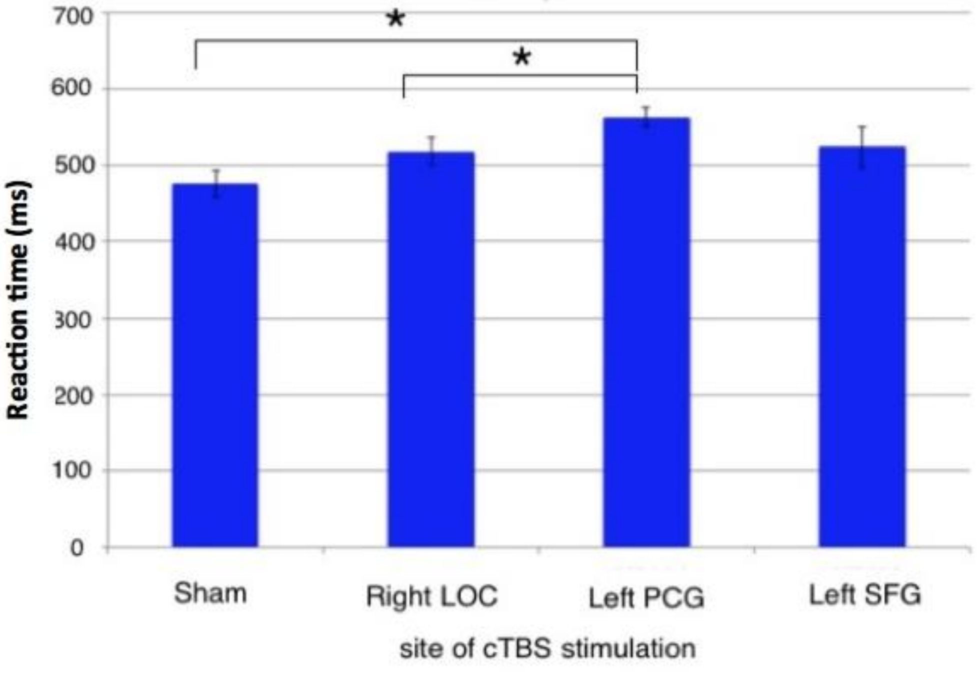


Figure 6.2 shows the mean reaction time during each cTBS session for the all change condition. The * denotes the sites of stimulation that led to a significant change in RT in contrast to the sham condition.

No change

The reaction time in the no change condition represents the time it takes to respond to a primed object. There was a main effect of cTBS across the NC condition, F(3,27)=5.918, P=0.003, η_p^2 = 0.397. cTBS to the right LOC, left PCG or the left SFG did not lead to any significant change in RT in contrast to the RT observed during the sham condition, P= 0.1, >0.99 and >0.99 respectively.

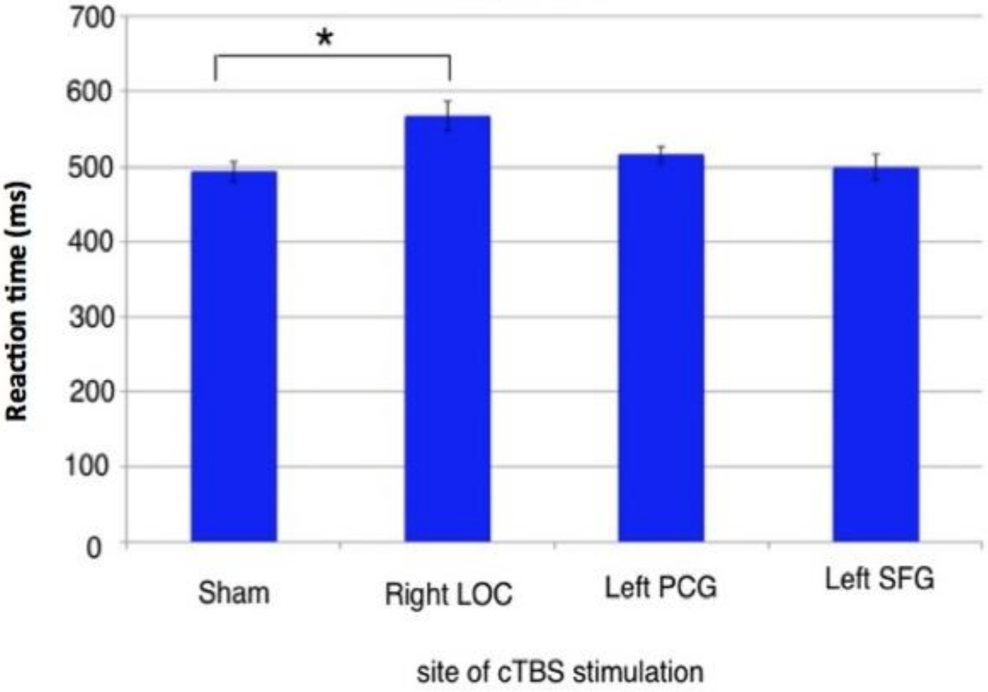


Figure 6.3 shows the mean reaction time during each cTBS session for the no-change condition. The * denotes the sites of stimulation that led to a significant change in RT in contrast to the sham condition.

Relevant feature change

There was no significant effect of cTBS on the RFC condition, F(3,27)=2.674, P=0.067, η_p^2 =0.229.

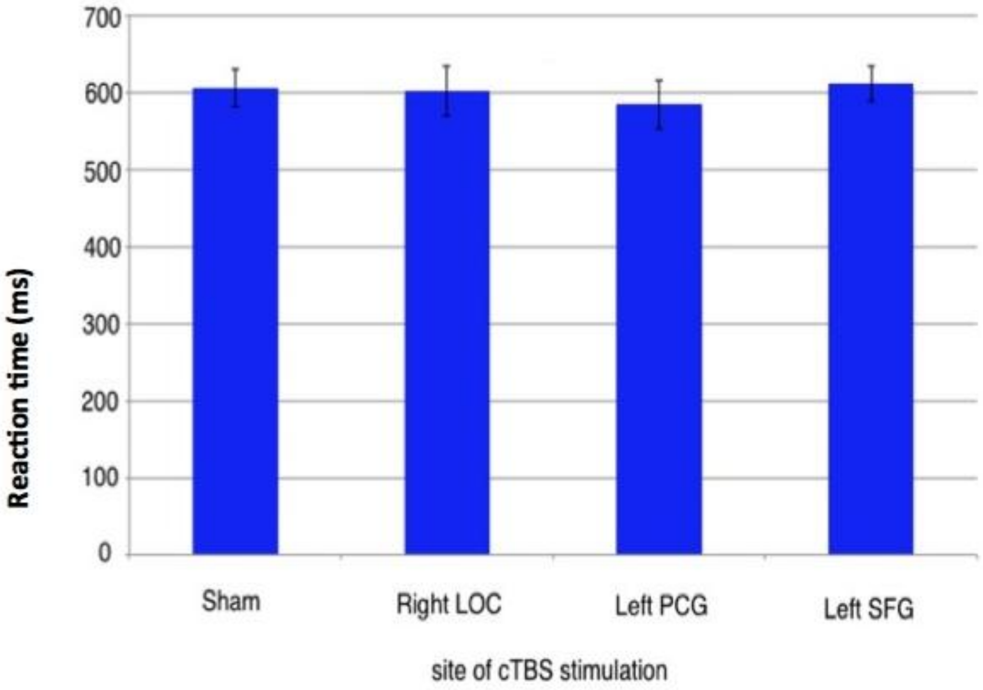


Figure 6.4 shows the mean reaction time during each cTBS session for the relevant feature change condition. The * denotes the sites of stimulation that led to a significant change in RT in contrast to the sham condition.

Irrelevant feature change

There was a significant main effect of cTBS across the IFC condition. F(3,27) = 13.205, P=<0.001, η_p^2 = 0.595. Following cTBS to the left SFG there was a significant decrease in RT in contrast to the sham condition (mean difference = 97.6ms, P=0.13, η_p^2 = 0.668). However, cTBS to the right LOC (P>0.99) or left PCG (P>0.99) did not lead to a significant change in RT.

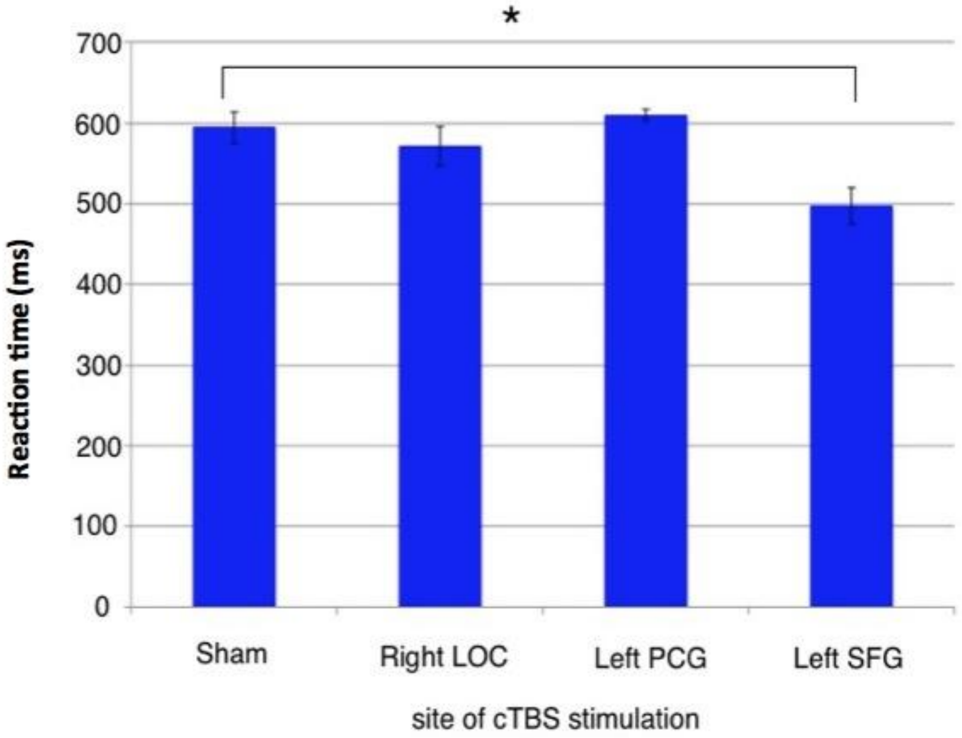


Figure 6.5 shows the mean reaction time during each cTBS session for the irrelevant feature change condition. The * denotes the sites of stimulation that led to a significant change in RT in contrast to the sham condition.

In summary cTBS to the right LOC and left PCG led to an increase in RT during the AC condition in contrast to the sham condition. In contrast to sham cTBS, cTBS to the left SFG led to a significant decrease in RT in response to the IFC condition. However, cTBS to the right LOC, left SFG and left PCG did not lead to any significant change in the RT during the RFC and the NC conditions.

6.5 Discussion

The results of experiment 5 show a critical role for the left SFG in the processing of task irrelevant features during the reviewing paradigm. In contrast to the hypotheses the results do not show a causal role for the right LOC or left PCG in the RFC condition, but instead show a critical role in the AC condition.

The results of experiment 4 suggested that there is a widespread fronto-parietal network that is engaged during the process of feature binding and object representation. It was expected that applying the inhibitory protocol of cTBS to the 3 key areas that showed an increase in BOLD during experiment 4 (right LOC/left SFG/left PCG) would allow us to selectively suppress neural mechanisms that may be integral to the rebinding and updating process. However, these preliminary results were not consistent with the fMRI results. It was predicted cTBS of the right LOC and left PCG, both of which showed increase in BOLD during the RFC condition in contrast to the AC condition, would lead to an increase in RT during the RFC condition and leave the RT in the AC condition unchanged. On the contrary, the results revealed an increase in RT in the AC condition only following cTBS to the right LOC and left PCG. There was no other significant change in RT following right LOC cTBS.

An explanation for this result may lay in the nature of the processes being recruited during each condition. For example, the RFC condition recruits perceptual and motor processes that are postulated to conflict with previously held perceptual and motor representations, due to the presentation of a similar object 680ms earlier. On the other hand, although the AC condition recruits both perceptual and motor functions, perceptual conflict should not occur as the object presented has completely changed in its appearance from the previously presented object 680ms ago. Therefore, it is possible that because the RFC condition engages more complex processes than the AC condition, that disruption of any one area is not sufficient to interfere with the overarching process and network that is recruited.

Although a number of studies investigating the maintenance of an object representation in the visual working memory have revealed a significant role for prefrontal regions (Ranganath et al. 2000; Sakai et al. 2002; Song and Jiang, 2006) and the LOC (Xu and Chun, 2006), these studies did not focus on the neural basis on updating a representation. The current task specifically recruits processes that update previously held representations with new information. Results from experiment 4 are consistent with the results observed by Schulte et al. (2009) which show that where a task leads to perceptual conflict a more frontal parietal network is engaged whereas motor conflict engages a more posterior network including the PCG.

In addition, a recent study carried out by Smith and Goodale (2014) provides further insight into the link between action and vision and an explanation as to why cTBS of the left PCG would lead to an increase of RT in the AC condition. Smith et al. (2014) investigated whether different visual images of common object categories would be reliably discriminated in early somatosensory cortex despite participants having no interactions with the visual stimuli during the experiment. Using fMRI, Smith et al. (2014) investigated whether different visual images of common object categories would be reliably discriminated in early somatosensory cortex, even without any interaction. It was predicted that this might be possible due to associative links that are formed through experience with specific objects. The results showed that the somatosensory cortex (PCG/S1) carries information that discriminates familiar object categories. This was the case even though subjects had no interaction with the ojects presented in the experiment, and neither did the static images depict any interaction. The authors conclude that cross modal connections from vision to early somatosensory cortex transmit content-specific information about familiar object categories based on visual appearance alone.

Smith et al. (2014) results also fit with the neuro-architectural framework (convergence divergence zone framework) proposed about the neural representation of perceptual experience (Damasio, 1989; Meyer & Damasio, 2009), which implies that early sensory areas (V1/S1) simultaneously represent perceptual information in either recall or recognition (Smith et al. 2014). Therefore inhibiting the PCG may have directly inhibited the perception of that object and/or the action afforded by that action. However, there was no evidence that this was happening during the RFC condition, which may indicate a different process being engaged during this condition.

Experiment 4 revealed a differentiation in cortical areas recruited, dependent on whether a relevant feature or irrelevant feature alternated between the presentation of S1 and S2. The neuroimaging results showed a large increase in BOLD in the left SFG during the IFC condition in contrast to the NC condition. The current study is able to confirm the causal role of this area in the IFC condition. There was a significant decrease in RT following cTBS to the left SFG as opposed to sham cTBS.

The observed disruption of the updating of an object representation following cTBS to the left SFG is consistent with studies that have shown that perceptual conflict engages a more frontal network (Schulte et al. 2009) and that the SFG is specifically integral to the monitoring and manipulation of perceptual information in VWM (du Boisgueheneuc, 2006). This is in contrast to the proposed low level and fast disintegrating processing that Xu (2010) proposed irrelevant features were subject to during object processing.

In conclusion, cTBS to the three distinct cortical areas spanning the occipital, parietal and frontal cortices caused a specific modulation of RT within both the IFC and AC condition. Inline with the hypothesis regarding the causal role of the left SFG during an irrelevant feature change update, the data shows that following an inhibitory protocol to the left SFG the RT during the IFC condition only significantly increases. The results following the application of cTBS to both the right LOC and left PCG were not inline with predictions and are inconclusive. As this study, to the best of my knowledge, is the first cTBS study carried out to specifically probe the processes engaged during the reviewing paradigm, further data needs to be collected in order to gain a clearer understanding of the network engaged. Further scope for study may lay in the use of strategically timed single pulse TMS to disrupt delayed processes at play when the bound representation is being updated during the RFC or IFC conditions.

Chapter 7 – General Discussion

The cortical network of visual feature binding

The aim of this thesis was to explore the process of feature binding, where different features such as location, shape, colour and motion are linked together to form a coherent representation of an object, with a specific focus on differentiating the cortical network associated with feature binding from the cortical regions of the brain associated with attention and other processes. Two paradigms were employed to achieve this objective. The first paradigm was developed to meet the unique demand of experiment 1. Experiment 1 aimed to contrast spatial detection, temporal attention and explicit feature binding in one paradigm, whilst keeping both task difficulty and low-level stimuli differences constant across conditions. In addition to exploring the cortical networks engaged during feature binding this paradigm allowed exploration of both spatial processing and temporal attention. In comparison to spatial processing, temporal attention is relatively unexplored, and this paradigm enabled a closer exploration of the conflicting models of temporal attention alongside the main research question.

The second paradigm, namely the reviewing paradigm (Kahneman et al. 1992), was employed in experiments 2a, 3 4 and 5. The reviewing paradigm provided a means to elicit implicit feature binding and therefore following the use of fMRI, enabled the detection of cortical areas engaged in the feature binding process. In contrast to the current literature experiment 2a reduced the stimuli down to two simple features; colour and motion. This modification aimed to control for possible confounds from using already complex stimuli (Keizer et al. 2008). The task then consisted of a simple feature detection choice being made on one of the features (i.e. motion) while the binding between both of the features (i.e. colour and motion) was being measured. However prior to the subject making the feature detection choice, a preview of an object was presented (S1). S1 also consisted of a selection of dots moving in a set direction (either up or down) and all one colour (either red or green). This object was deemed irrelevant by task instruction and participants were instructed to just observe the object and wait for the appearance of the second object (S2) prior to response.

The focus of experiment 2a was to measure the change in the RT performance when a feature, rendered irrelevant through task instruction (colour) was either alternated or remained identical between S1 and S2. The difference in the RT between a condition where only colour alternated between S1 and S2 and a condition where both colour and motion remained the same between S1 and S2 was termed the irrelevant feature change cost (IFCC). Two further conditions were included: when only the relevant feature (motion) alternated between S1 and S2 or when all features alternated (both motion and colour) between S1 and S2. The difference in RT when a relevant feature alternated in contrast to when all features alternated was termed the relevant feature change cost (RFCC). The absence of the IFCC and RFCC would indicate that participants could ignore the irrelevant features and attend only to the relevant features, in accordance with task instructions. Reduced performance (increased RT) during the RFC condition and IFC condition, which in turn would lead to a larger RFCC and IFCC, would indicate that all features automatically participate in the initial representation of an object, even if they are irrelevant to the task. Furthermore, the presence of an RFCC and IFCC suggest that when features change between two representations that are considered, by the visual system, to be a continuation of one object, an updating process takes places in which the previous object representation is updated with the new information that has been presented to the system. Using this paradigm we were able to observe the network engaged during the implicit binding and updating process.

Feature binding versus attention

Previous studies using the visual search paradigm have led to the assertion that it is the ability to focus spatial attention that allows us to bind features together into well-defined mental representations (Treisman et al. 1980; Albert et al. 2013). The feature integration theory (FIT) proposes that visual feature binding requires accurate spatial information (Treisman et al. 1980; Robertson, Treisman, Friedman-Hill & Grabowecky, 1997). The spatial information that appears critical for feature binding proposed by the FIT has been linked to parietal function (Friedman-Hill, Robertson and Treisman, 1995). Therefore it has been suggested that interactions between parietal areas and lower cortical areas such as V4 and MT are necessary for resolving the binding problem (Robertson, 1999).

Empirical support for the FIT has been gained through several observations. First, visual detection of the presence or absence of a feature produces RTs that are independent of the number of distractors in the display; however, the detection of a conjunction creates an increasing RT, correlating with the increasing number of distractors. Therefore it was argued that when participants have to find a target, spatial attention is engaged and a serial spatial search entails (Treisman & Gelade, 1980). Feature binding errors, termed illusory conjunctions, are seen when items are presented for a brief time and attention is divided or diverted (Prinzmetal, Presti & Posner, 1986; Treisman & Schmidt, 1982). According to FIT, attentional allocation to a location is necessary to properly bind features together, and although this model has received a remarkable level of support, studies indicate that when spatial attention is impaired or not relevant that we are still able to bind features together successfully, especially if the participants can engage temporal attention (Robertson, 1999). Furthermore, binding has been shown to take place without attention or awareness (Melcher et al. 2005).

Experiment 1 contrasted spatial and temporal based judgements to an explicit feature binding task which involved participants reporting the specific combination of colour and motion. A whole brain analysis and retinotopic mapping was carried out to allow a thorough analysis of the whole brain during each of the three tasks. It was hypothesised that we would see previously established cortical areas engaged during spatial detection and temporal attention; however, I hypothesised that in the feature-specific areas of V4 and MT we would see a specific increase of BOLD during the explicit feature binding task. The data did not support this: retinotopic visual areas showed a significant increase in BOLD during the spatial task only, with no unique observable signature associated with the explicit feature binding task.

On further reflection it seems plausible that the reason this experiment failed to reveal an explicit feature binding network was either because the cortical areas recruited were subsumed within the spatial processing network, or the explicit feature binding task was engaging spatial and temporal processing, or more likely, the spatial and temporal task also led to feature binding taking place. The latter explanation is consistent with the model of integrated competition of attention (Duncan, 1984; Luck and Vogel, 1997; Scholl, 2001) which posits that when attention is directed to an objects feature all other features of that object may be registered, even when those unattended features are also irrelevant (O'Craven et al. 1999). Therefore it became evident that the paradigm developed for experiment 1 was not suitable for observing and measuring visual feature binding.

In experiment 2 the reviewing paradigm was introduced. This task allowed the measurement of the impact of feature binding, for which there was no explicit task demand to do so and the window in which attention could be engaged was brief (680ms).

Object files and spontaneous feature binding

For consistency, colour and motion were the chosen features to be used during the reviewing paradigm. As the RFCC and IFCC have been previously established (Kahneman et al. 1992; Hommel, 1998, 2004, 2008) the initial experiment sought to test the parameters that allowed the secondary presentation of an object (S2) to be seen as a continuation of the first object (S1).

Previous research suggests that conceptual priming between words and objects is common (Hirshman et al. 1990; Weldon, 1993). The main aim of experiment 2B was to assess whether an object file would encompass conceptual information about features, for example whether S1 consisted of the word red or the colour red would affect the IFCC observed. If an RFCC or an IFCC was observed this would suggest that when an object is bound then its conceptual counterparts are also primed, therefore the words "red" and "up" should lead to an IFC RT cost if the object that appeared consisted of green dots moving up. If no information regarding the conceptual nature of the object were held within the object file then it would not be expected to produce any change in the RT across conditions.

The results did not show any change in RT across conditions suggesting that an object file may be purely data driven and that cross modal priming does not lead to reactivation of a previous representation. An explanation for this may lie in the difference between retrieval processes for implicit and explicit retrieval processes (Lombardi et al. 2010). Lombardi (2010) suggests that implicit retrieval processes automatically retrieves information that provides a good match to the target, however explicit retrieval processes operate as an intentional retrieval set to access particular categories or types of memory information. As per the object file theory, in order to observe a binding cost such as an IFCC or an RFCC the S2 image must implicitly evoke the retrieval of the initial object. Therefore if implicit retrieval looks for the best match physically then it is unlikely that red upward moving dots will lead to the retrieval of the words red and up.

However, the null results observed in experiment 2B should be interpreted with care as experiment 2A failed to replicate standard feature change costs. It was concluded that this might be due to two ignored features namely shape and location of the dots. Therefore the reviewing paradigm was adapted for experiment 3.

In experiment 3 there was one relevant feature: motion. Three other features (location, colour and shape) could alternate between S1 and S2 however all three features were classed as irrelevant. In order to explore the role of features within the formation and retrieval of an object representation, 4 separate sessions of testing were carried out in which the relevant feature changed to one of the four possible features. Participants were then told to attend explicitly to this feature only and ignore all other features.

In experiment 2A, we failed to produce any IFCC or RFCC. However, following the inclusion and control of location and shape information, these effects emerged. Both an RFCC and an IFCC was observed, supporting the idea that, irrespective of whether the partial repetition of an object was due to a task relevant or task irrelevant feature change, an object file was retrieved and updated.

A further point of investigation was whether location, motion, colour and shape would lead to equal partial repetition costs, either as relevant or irrelevant features in the display. The role of location information has previously been a point of contention. Kahneman et al. (1992) stress the importance of location in the creation and retrieval of an object file. However, Van Dam et al. (2010) argue that it was unclear whether RT benefits were the result of previewing a particular area of space, or previewing those features within that space. Further to this, evidence from attentional studies (Hommel 1998, 2007; Hommel & Colzato, 2004) and developmental studies (Leslie, Xu, Tremoulet

& Scholl, 1998) suggest that feature bindings do not necessarily need to include spatial codes in order to be retrieved.

These results suggest that all features do not play an equal role, but instead task salience modulates the impact of feature alternation of object representation. Although location did produce robust IFCC and RFCC, if location information was the only way in which object files could become reactivated you would not expect to see a RFCC in any other block.

An alternative explanation for the seemingly equal role of location as a feature may lie in the fact that there was only ever one object. Episodic retrieval via non-spatial features has been demonstrated in previous research, however, like this experiment, there was only one object (Colzato, Raffone, & Hommel, 2006; Hommel, 1998; Hommel, & Colzato, 2004). Therefore, when multiple objects are present, spatial correspondence may be integral to deal with the spatial uncertainty (Kahneman, Treisman & Gibbs, 1992; Mitroff & Alvarez, 2007; Saiki, 2003).

The 'Simon Effect' and the 'Spatial Stroop Effect' have been identified as a factor leading to the assignment of location as an important status. The 'Simon Effect' (Craft & Simon, 1970) is seen when participants are asked to respond to a non-spatial feature in a binary choice task with a left and right assigned key response. A faster RT is observed when the key response is congruent with the side of the screen that the object appears on. Similarly, the 'Spatial Stroop Effect' (MacLeod, 1991) is observed when the subject must respond to a word that has spatial information (e.g. right or left) with a right or left key response. Although location information is irrelevant during the task, the location of the spatial word significantly modulates the RT to that word. This is not to imply that location information is not of a special status within perception.

Results also showed that there was significant effect of feature, therefore participants did not respond to all features equally; attending to location did yield a faster response time than attending to shape. This suggests that location is processed at a higher speed than non-spatial features and may play an integral role in the encoding of object files. The neural mechanisms underlying the impaired performance, observed after partial repetitions of objects, are unknown. It is assumed that this impairment happens due to the conflict between the retrieved and perceptually available features and/or because the old associations need to be deconstructed (Colzato, van Wouwe, Lavender & Hommel, 2006)

The results from experiment 3 showed robust partial repetition costs following both relevant and irrelevant feature changes. This provided confirmation that feature binding was taking place upon viewing S1 and then an updating of that feature binding was taking place upon viewing S2.

Object files and the cortical network of feature binding

In order to return to the main research aim, the reviewing paradigm was then performed during fMRI. Keizer et al. (2008) carried out an fMRI study using the reviewing paradigm and a stimulus made up of three types of neurally dissociable components: faces, houses and movement. Participants were presented with preview displays (S1) and targets (S2) that both consisted of blended images of a house and a face. The house or the face moved in one of two possible directions. Participants were to respond to the direction of S2, irrespective of what object moved. Of particular interest were the conditions where S1 showed a moving house and S2 a moving face; if the direction of motion in these two displays was the same (i.e. the motion feature was repeated) the PPA was more active than if the motion direction alternated. Therefore, repeating the motion feature during S2 led to the retrieval of the object that moved during S1 (house) and hence led to an increase in activation within the PPA. This showed evidence that repeating a feature can reactivate the neural code of this feature, which then spreads activation to the other feature codes that it is still bound to. However, Keizer et al. (2008) failed to mirror this effect in the FFA; no significant increase in BOLD was observed in trials where the repetition of the motion direction should have led to a reactivation of the previously bound face, even though, behaviourally, the partial repetition cost was present. Due to the complex stimuli that Keizer et al. (2008) employed in their paradigm, it is difficult to interpret the partial null result. As it is established that faces are processed faster and to a much higher level than other objects (Roisson & Gauthier, 2002), one could argue that it is not unusual that the pattern of BOLD observed in the PPA was not mirrored in the FFA.

In contrast to Keizer et al. (2008) experiment 4 entailed a whole brain analysis to determine whether a task RFC would engage a different cortical network than a task IFC. Alongside a whole brain analysis, an ROI analysis was carried out on area MT to establish whether we would see an increase of BOLD that correlates with the increase in the partial repetition cost observed behaviourally. We also tested whether individual differences in IFCC and RFCC correlated with individual difference in the BOLD signal in area V5/MT. The predicted behavioural result was replicated and a significant increase in RT was observed when either a task relevant or irrelevant feature was alternated relative to the AC and the NC, respectively.

Results from this experiment showed that updating an object with a change in either a relevant or irrelevant feature recruited a wide range of areas across the parietal, occipital and frontal cortices. Due to the matching of motor demands across the tasks the RFC condition was never directly contrasted to the IFC condition. For this reason it was not possible to draw direct comparisons between the cortical networks engaged during the RFC and the IFC. However in response to an IFC vs NC we did observe activation in the right and left LOC and the left SFG. However the activation observed following a RFC vs AC contrast was in the right LOC and left PCG only.

In contrast to experiment 1, where no unique cortical areas of activation were observed in response to the explicit binding task, experiment 4 revealed increased BOLD across the left MFG, SFG and bilateral IPS and LOC in response to a task that elicited implicit feature bidning. It was postulated that the lack of BOLD in response to an explicit feature-binding task maybe due to the feature binding network becoming subsumed within the cortical areas engaged during the spatial and temporal detection tasks. During experiment 1 these were also areas where activation was observed during the spatial and temporal detection tasks. While this overlap could indicate a shared mechanism of action, I am unable to conclude this from the null- effect observed in the data. The data may imply that the cortical areas engaged during explicit feature binding are also engaged during a spatial detection and temporal processing task.

As in experiment 1, an ROI analysis was undertaken on area MT. In experiment 4 it was hypothesized that area MT may show an increase of BOLD during the IFC condition that correlated on an individual level with the IFCC. However this was not the case and there was no correlation. Further to this, area MT showed no significant increase in the BOLD level during the conditions in which a RT cost was incurred, in contrast to the conditions in which no RT cost was observed. This along with the results of experiment 1 suggest that area MT does not play a specific role in feature binding even when motion is the featuring that is being bound. This runs contrary to a fMRI study carried out by Seymour et al. (2009) in which MVPA was employed during the analysis to look for areas that were showed processing of the conjunction of colour and motion. The results showed that information regarding the processing of the conjunction of colour and motion was present through in V5/MT. However, when they carried out a univariate analysis, as was done in experiment 1 and experiment 4 of this thesis they fail to find any preferential activation of the lower cortical areas such as V5/MT. Therefore the lack of significant BOLD being observed in the lower visual areas may be accounted for by the analysis method. This may be a question that can be addressed future research.

It is worth noting that fMRI results indicate areas that show an increase in BOLD in correlation with the completion of a task. In order to probe the direct and specific roles of these cortical areas in the rebinding and updating process, cTBS was employed as an interference method. Following the application of cTBS to either the right LOC, left SFG or left PCG, participants carried out the reviewing paradigm task in an identical format to the previous fMRI experiment (4).

The number of participants tested in experiment 5 was modest and therefore the results are preliminary. It was hypothesised that applying cTBS to the right LOC would lead to an increase in the RT during both the RFC and IFC conditions but not the NC and AC conditions. It was hypothesised that applying cTBS to the left PCG would lead to an increase during the RFC and cTBS to the left SFG would lead to a significant increase in the RT during the IFC condition only. This would then lend further evidence to the supposition that these areas play a causal role specifically under conditions in which binding is known to take place.

The results of experiment 5 were not consistent with the fMRI results of experiment 4. Results showed that cTBS to the left PCG and right LOC increased RT during the AC condition only. This was at odds with the fMRI data in experiment 4, which revealed an increase of BOLD activity in response to the RFC vs AC in both the right LOC and left PCG. However, the observation that cTBS to the left SFG led to a reduced reaction time to an IFC condition was consistent with the fMRI data of experiment 4. This demonstrates that this area is selectively involved in rebinding process when an irrelevant feature is being updated.

Conclusions

The over-arching goal of the thesis was to explore the neural networks and neurocognitive mechanisms that are recruited during visual feature binding. The work described in early chapters of this thesis suggest that cortical areas associated with explicit feature binding tasks can be inseparable from those recruited during either temporal or spatial attention. In the chapters 3, 4, 5 and 6 it becomes clear that viewing an object or a co-occurrence of features led a spontaneous binding of those features. The conclusions from the behavioural results seen in experiments 2, 3, 4 and 5 may provide an explanation for the lack of BOLD observed in experiment 1 in response to a feature binding task. Furthermore, experiments 2, 3, 4 and 5 provide further evidence of an automatic object based mechanism of selective attention (O'Craven et al.1999). To explain this processing benefit, previous researchers have often argued that different object features can be processed and retained independently, meaning that the RT benefit results from features not competing with each other for the same processing resources. This suggests that an irrelevant feature of an attended object can be registered for 'free' (Wheeler and Treisman, 2002; Xu, 2002a). However the results observed following the completion of the reviewing paradigm does not support this hypothesis. The results presented here suggest that a task irrelevant feature is integrated spontaneously with task relevant features and that a partial repetition of those bound features leads to an increase in RT whether or not the feature is task relevant. This suggests that the features are no longer independent from each other. However, the neuroimaging results of experiment 4 do support previous findings (Xu,

2010) that processing of a task irrelevant feature does take a different cortical path and therefore results in a different neural fate than task relevant features.

The neural correlates that were observed following whole brain analysis in experiment 4 currently stand alone in the respect that only ROI analyses have been carried out in conjunction with the reviewing paradigm, therefore further replication is needed. This is also true of the application of cTBS to cortical areas engaged during the RFC and IFC conditions. Moving forward, the application of online TMS would be of interest in probing the formation and updating of object files. For example, if the RFCC and IFCC represent the formation of an object file then the application a single pulse during the viewing of S1 may interrupt the formation of an object file and hence no partial repetition cost (or a reduced cost) would be predicted irrespective of which feature was alternated.

In contrast to previous research in which either the visual cortex (Seymour et al. 2010; Golledge 2003) or parietal cortex (Shafritz et al. 2002; Albert, Sheremata, Silver and Robertson, 2013) has been then main focus of study, this thesis turned its attention to the whole brain. Results have shown that as with higher cognitive functions such as attention and temporal order judgements, something as fundamental as binding colour, shape and motion engages a widespread network and recruits areas that are otherwise associated with high-level processes such as the SFG.

In summary this thesis has made several important empirical contributions. By creating a paradigm in which spatial, temporal and feature conjunction tasks can be contrasted while controlling for low level stimuli differences and task difficulty. The results of this experiment allowed previous contradictions within the literature surrounding temporal and spatial processing to be addressed. The following chapters move the focus to implicit feature binding in which an established paradigm is adapted in order to make several important contributions. In experiment 2a, an irrelevant feature change is contrasted to a relevant feature change, which in contrast to previous literature enables the observation of the differing of impact on the RT dependent on whether the feature is relevant or not. In experiment 3, the paradigm is adapted further and the stimulus alternates on four feature dimensions. This then enables the contrast between the RT impact of changing different features when either relevant or irrelevant to the task. Following this, the reviewing paradigm is combined with fMRI for the second time in the literature. However, the stimulus was reduced to low-level stimulus in order to avoid the confounds of the previous experiment (Keizer et al. 2008) in which already complex stimuli was used.

Experiment 5 then combines the reviewing paradigm with cTBS for the first time in order to probe the causal influence of those areas showing increased BOLD during experiment 4. As discussed above these results need further development and this is important for future research.

The important question moving forward is how the brain achieves synchrony. It has been suggested that gamma oscillations may be a mechanism by which the brain coordinates many areas across the brain. Future studies may benefit from increasing use of concurrent EEG-TMS. The use of rhythmic TMS will allow this hypothesis to be tested.

Bibliography

Albert, R. A. Sheremata, S. L. Silver, M. A. & Robertson, L. C. (2013). The role of the parietal cortex in feature binding in visual search. *Journal of Vision*, *13*(9), 158–158. doi:10.1167/13.9.158

Allport, D A. Tipper, S. P. & Chmiel, N. (1985). Allport, Topper & Chmiel. In *Perceptual integration and post-categorical filtering. In M. I. Posner & O. S. M. Marln (Eds.), Attention and performance X1* (pp. pp. 107–132). Hillsdale, NJ: Erlbaum.

Amorapanth, P. X. Widick, P. & Chatterjee, A. (2010). The neural basis for spatial relations. *Journal of Cognitive Neuroscience*, *22*(8), 1739–1753. doi:10.1162/jocn.2009.21322

Anderson, J. R. (n.d.). *Cognitive psychology and its implications (3rd ed.). A series of books in psychology.*

Arguin, M. Cavanagh, P. & Joanette, Y. (1994). Visual feature integration with an attention deficit. *Brain and Cognition*, *24*(1), 44–56. doi:10.1006/brcg.1994.1003

Arnold, D. H. (2005). Perceptual pairing of colour and motion. *Vision Research*, *45*(24), 3015–26. doi:10.1016/j.visres.2005.06.031

Arrington, C. M. Carr, T. H. Mayer, A. R. & Rao, S. M. (2000). Neural mechanisms of visual attention: object-based selection of a region in space. *Journal of Cognitive Neuroscience*, *12 Suppl 2*, 106–17. doi:10.1162/089892900563975

Article, S. (2008). On the neural basis of fMRI signals. *Nature Neuroscience*, *119*, 729–730. doi:10.1016/j.clinph.2007.10.025

Ashbridge, E. (1997). Temporal aspects of visual search studied by transcranial magnetic stimulation. *Neuropsychologia*, *35*(8), 1121–1131. doi:10.1016/S0028-3932(97)00003-1

Ashbridge, E. Cowey, A. & Wade, D. (1999). Does parietal cortex contribute to feature binding? *Neuropsychologia*, *37*(9), 999–1004.

Ashbridge, E. Cowey, A. & Wade, D. (1999). Does parietal cortex contribute to feature binding? *Neuropsychologia*, *37*(9), 999–1004.

Ashbridge, E. Walsh, V. & Cowey, A. (1997). Temporal aspects of visual search studied by transcranial magnetic stimulation. *Neuropsychologia*, *35*(8), 1121–31.

Attention, O. (2005). Space- and Object-Based Attention. *Foundations*, *124*(6), 130–134. doi:10.1016/B978-012375731-9/50027-6

Attention, S. (2005). Spatial Attention. *Foundations*, 407–411.

Attwell, D. & Iadecola, C. (2002). The neural basis of functional brain imaging signals. *Trends in Neurosciences*, *25*(12), 621–625. doi:10.1016/S0166-2236(02)02264-6

Baars, B. (1988). *A cognitive theory of consciousness*. New York: Cambridge University Press.

Baciu, M. Koenig, O. Vernier, M. P. Bedoin, N. Rubin, C. & Segebarth, C. (1999). Categorical and coordinate spatial relations: fMRI evidence for hemispheric specialization. *Neuroreport*, *10*(6), 1373–8.

Baddeley, A. (1996). The fractionation of working memory. *Proceedings of the National Academy of Sciences*, *93*(24), 13468–13472.

Barker, A. T. Freeston, I. L. Jabinous, R. & Jarratt, J. A. (1986). Clinical evaluation of conduction time measurements in central motor pathways using magnetic stimulation of human brain. *Lancet*, *1*(8493), 1325–6.

Bartels, A. Munk, M. & Schultz, J. (2010). Physiological and Physical Basis of Functional Brain Imaging. *October*, (October).

Bartels, A. & Zeki, S. (2000). The architecture of the colour centre in the human visual brain: new results and a review. *The European Journal of Neuroscience*, *12*(1), 172–93.

Bartels, A. & Zeki, S. (2006). The temporal order of binding visual attributes. *Vision Research*, *46*(14), 2280–6. doi:10.1016/j.visres.2005.11.017

Battelli, L. Pascual-leone, A. & Cavanagh, P. (2007). The “ when ” pathway of the right parietal lobe, *11*(5). doi:10.1016/j.tics.2007.03.001

Battelli, L. Pascual-Leone, A. & Cavanagh, P. (2007). The “when” pathway of the right parietal lobe. *Trends in Cognitive Sciences*, *11*(5), 204–10. doi:10.1016/j.tics.2007.03.001

Baylis, G. C. & Driver, J. (1993). Visual attention and objects: Evidence for hierarchical coding of location. *Journal of Experimental Psychology: Human Perception and Performance*, *19*(3), 51–470.

Benali, A. Trippe, J. Weiler, E. Mix, A. Petrasch-Parwez, E. Girzalsky, W. … Funke, K. (2011). Theta-burst transcranial magnetic stimulation alters cortical inhibition. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, *31*(4), 1193–203.

Berti, A. & Rizzolatti, G. (1992). Visual Processing without Awareness: Evidence from Unilateral Neglect. *Journal of Cognitive Neuroscience*, *4*(4), 345–51. doi:10.1162/jocn.1992.4.4.345

Bisiach, E. Cornacchia, L. Sterzi, R. & Vallar, G. (1984). Disorders of perceived auditory lateralization after lesions of the right hemisphere. *Brain : A Journal of Neurology*, *107 (Pt 1*, 37–52.

Bjoertomt, O. Cowey, A. & Walsh, V. (2002). Spatial neglect in near and far space investigated by repetitive transcranial magnetic stimulation. *Brain : A Journal of Neurology*, *125*(Pt 9), 2012–22.

Bohbot, V. D. Kalina, M. Stepankova, K. Spackova, N. Petrides, M. & Nadel, L. (1998). Spatial memory deficits in patients with lesions to the right hippocampus and to the right parahippocampal cortex. *Neuropsychologia*, *36*(11), 1217–1238. doi:10.1016/S0028-3932(97)00161-9

Botvinick, M. M. Cohen, J. D. & Carter, C. S. (2004). Conflict monitoring and anterior cingulate cortex: an update. *Trends in Cognitive Sciences*, *8*(12), 539–46. doi:10.1016/j.tics.2004.10.003

Bouvier, S. & Treisman, A. (2010). Visual feature binding requires reentry. *Psychological Science*, *21*(2), 200–4. doi:10.1177/0956797609357858

Braet, W. & Humphreys, G. W. (2009). The role of reentrant processes in feature binding: Evidence from neuropsychology and TMS on late onset illusory conjunctions. *Visual Cognition*, *17*(1-2), 25–47. doi:10.1080/13506280802193318

Brass, M. Bekkering, H. Wohlschläger, A. & Prinz, W. (2000). Compatibility between Observed and Executed Finger Movements: Comparing Symbolic, Spatial, and Imitative Cues. *Brain and Cognition*, *44*(2), 124–143.

Brewer, A. A. Press, W. A. Logothetis, N. K. & Wandell, B. A. (2002). Visual Areas in Macaque Cortex Measured Using Functional Magnetic Resonance Imaging, *22*(v), 6–15.

Broadbent, D. E. (1958). *Perception and communication* (p. 338). Pergamon Press.

Brockmole, J. R. & Franconeri, S. (2009). Binding: a special issue of visual cognition. *Psychology Press*, *17*(1-2).

Bullinaria, J. A. (1994). Simulating nonlocal systems: Rules of the game. *Behavioral and Brain Sciences*, *17*(01), 61–62.

Burr, D. McKee, S. & Morrone, C. M. (2006). Resolution for spatial segregation and spatial localization by motion signals. *Vision Research*, *46*(6-7), 932–9. doi:10.1016/j.visres.2005.09.025

Burr, D. & Morrone, C. (2006a). Perception: transient disruptions to neural space-time. *Current Biology : CB*, *16*(19), R847–9. doi:10.1016/j.cub.2006.08.075

Burr, D. & Morrone, C. (2006b). Time perception: space-time in the brain. *Current Biology : CB*, *16*(5), R171–3. doi:10.1016/j.cub.2006.02.038

Cárdenas-Morales, L. Nowak, D. A. Kammer, T. Wolf, R. C. & Schönfeldt-Lecuona, C. (2010). Mechanisms and applications of theta-burst rTMS on the human motor cortex. *Brain Topography*, *22*(4), 294–306. doi:10.1007/s10548-009-0084-7

Case Studies in the Neuropsychology of Vision. (1999) (p. 210). Psychology Press.

Categorical and coordinate spatial relations:fMRI evidence for hemispheric specialization. (n.d.).

Cavanagh, P. & Alvarez, G. A. (2005). Tracking multiple targets with multifocal attention. *Trends in Cognitive Sciences*, *9*(7), 349–54. doi:10.1016/j.tics.2005.05.009

Cave, K. R. & Bichot, N. P. (1999). Visuospatial attention: Beyond a spotlight model. *Psychonomic Bulletin & Review*, *6*(2), 204–223. doi:10.3758/BF03212327

Cave, K. R. & Bichot, N. P. (1999). Visuospatial attention: beyond a spotlight model. *Psychonomic Bulletin & Review*, *6*(2), 204–23.

Chambers, C. D. Payne, J. M. Stokes, M. G. & Mattingley, J. B. (2004). Fast and slow parietal pathways mediate spatial attention. *Nature Neuroscience*, *7*(3), 217–8. doi:10.1038/nn1203

Chambers, C. D. Stokes, M. G. & Mattingley, J. B. (2004a). Modality-specific control of strategic spatial attention in parietal cortex. *Neuron*, *44*(6), 925–30. doi:10.1016/j.neuron.2004.12.009

Chambers, C. D. Stokes, M. G. & Mattingley, J. B. (2004b, November 21). Modality-Specific Control of Strategic Spatial Attention in Parietal Cortex. *Neuron*. Elsevier. doi:10.1016/j.neuron.2004.12.009 <http://dx.doi.org/10.1016/j.neuron.2004.12.009>

Chen, R. Classen, J. Gerloff, C. Celnik, P. Wassermann, E. M. Hallett, M. & Cohen, L. G. (1997). Depression of motor cortex excitability by low-frequency transcranial magnetic stimulation. *Neurology*, *48*(5), 1398–1403. doi:10.1212/WNL.48.5.1398

Chen, Z. (2009). Not all features are created equal: Processing asymmetries between location and object features. *Vision Research*, *49*(11), 1481–91. doi:10.1016/j.visres.2009.03.008

Chen, Z. & Yeh, Y.-Y. (2013). Perceived Object Continuity and Spontaneous Retrieval of Features from an Inhibited Object. *PLoS ONE*, *8*(5), e63264. doi:10.1371/journal.pone.0063264

CINEL, C. & HUMPHREYS, G. W. (2006). On the relations between implicit and explicit spatial binding: Evidence from Balint's syndrome. *Cognitive, Affective, & Behavioral Neuroscience*, *6*(2), 127–140. doi:10.3758/CABN.6.2.127

Cinel, C. Humphreys, G. W. & Poli, R. (n.d.). Cross-modal illusory conjunctions between vision and touch.

Clifford, C. W. G. Spehar, B. & Pearson, J. (2004). Motion transparency promotes synchronous perceptual binding. *Vision Research*, *44*(26), 3073–80. doi:10.1016/j.visres.2004.07.022

Cohen, A. & Ivry, R. B. (1991). Density effects in conjunction search: evidence for a coarse location mechanism of feature integration. *Journal of Experimental Psychology. Human Perception and Performance*, *17*(4), 891–901.

Cohen, A. & Rafal, R. D. (1991). ATTENTION AND FEATURE INTEGRATION: ILLUSORY CONJUNCTIONS IN A PATIENT WITH A PARIETAL LOBE LESION. *Psychological Science*, *2*(2), 106–110. doi:10.1111/j.1467-9280.1991.tb00109.x

Cohen Kadosh, R. & Henik, A. (2006). A Common Representation for Semantic and Physical Properties: A Cognitive-Anatomical Approach. *Experimental Psychology*, *53*(2), 87–94.

Colzato, L. S. Raffone, A. & Hommel, B. (n.d.). What do we learn from binding features? Evidence for multilevel feature integration.

Colzato, L. S. Warrens, M. J. & Hommel, B. (2006). Priming and binding in and across perception and action: a correlational analysis of the internal structure of event files. *Quarterly Journal of Experimental Psychology (2006)*, *59*(10), 1785–1804.

Colzato, L. S. Wouwe, N. C. Lavender, T. J. & Hommel, B. (2006). Intelligence and cognitive flexibility: Fluid intelligence correlates with feature “unbinding” across perception and action. *Psychonomic Bulletin & Review*, *13*(6), 1043–1048. doi:10.3758/BF03213923

Corbetta, M. (1993). Positron emission tomography as a tool to study human vision and attention. *Proceedings of the National Academy of Sciences of the United States of America*, *90*(23), 10901–3.

CORBETTA, M. AKBUDAK, E. CONTURO, T. SNYDER, A. OLLINGER, J. DRURY, H. … VANESSEN, D. (1998). A Common Network of Functional Areas for Attention and Eye Movements. *Neuron*, *21*(4), 761–773. doi:10.1016/S0896-6273(00)80593-0

Corbetta, M. Kincade, M. J. Lewis, C. Snyder, A. Z. & Sapir, A. (2005). Neural basis and recovery of spatial attention deficits in spatial neglect. *Nature Neuroscience*, *8*(11), 1603–10. doi:10.1038/nn1574

Corbetta, M. Miezin, F. M. Shulman, G. L. & Petersen, S. E. (1993a). A PET study of visuospatial attention. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, *13*(3), 1202–26.

Corbetta, M. Miezin, F. Shulman, G. & Petersen, S. (1993b). A PET study of visuospatial attention. *J. Neurosci. 13*(3), 1202–1226.

Corbetta, M. Miezin, F. Shulman, G. & Petersen, S. (1993c). A PET study of visuospatial attention. *J. Neurosci. 13*(3), 1202–1226.

Corbetta, M. Patel, G. & Shulman, G. L. (2008). The reorienting system of the human brain: from environment to theory of mind. *Neuron*, *58*(3), 306–24. doi:10.1016/j.neuron.2008.04.017

Corbetta, M. & Shulman, G. L. (2002). Control of goal-directed and stimulus-driven attention in the brain. *Nature Reviews. Neuroscience*, *3*(3), 201–15. doi:10.1038/nrn755

Corbetta, M. Shulman, G. L. Miezin, F. M. & Petersen, S. E. (1995). Superior Parietal Cortex Activation During Spatial Attention Shifts and Visual Feature Conjunction. *Science*, *270*(5237), 802–805. doi:10.1126/science.270.5237.802

Correa, Á. Sanabria, D. Spence, C. Tudela, P. & Lupiáñez, J. (2006). Selective temporal attention enhances the temporal resolution of visual perception : Evidence from a temporal order judgment task, *0*, 5–8.

Coull, J. . Frith, C. . Büchel, C. & Nobre, A. . (2000). Orienting attention in time: behavioural and neuroanatomical distinction between exogenous and endogenous shifts. *Neuropsychologia*, *38*(6), 808–819.

Coull, J. T. (2004a). fMRI studies of temporal attention: allocating attention within, or towards, time. *Brain Research. Cognitive Brain Research*, *21*(2), 216–26. doi:10.1016/j.cogbrainres.2004.02.011

Coull, J. T. (2004b). fMRI studies of temporal attention: allocating attention within, or towards, time. *Brain Research. Cognitive Brain Research*, *21*(2), 216–26. doi:10.1016/j.cogbrainres.2004.02.011

Coull, J. T. & Nobre, A. C. (1998). Where and When to Pay Attention: The Neural Systems for Directing Attention to Spatial Locations and to Time Intervals as Revealed by Both PET and fMRI. *J. Neurosci. 18*(18), 7426–7435.

Coull, J. T. Walsh, V. Frith, C. D. & Nobre, A. C. (2003). Distinct neural substrates for visual search amongst spatial versus temporal distractors. *Brain Research. Cognitive Brain Research*, *17*(2), 368–79.

Craft, J. L. & Simon, J. R. (1970). Processing symbolic information from a visual display: Interference from an irrelevant directional cue. *Journal of Experimental Psychology,*, *83*(3 (Pt. 1)), 415–420.

Cragg, B. G. (1969). The topography of the afferent projections in the circumstriate visual cortex of the monkey studied by the Nauta method. *Vision Research*, *9*, 733–747.

Craighero, L. Fadiga, L. Umiltà, C. A. & Rizzolatti, G. (1996). Evidence for visuomotor priming effect. *Neuroreport*, *8*(1), 347–9.

Crick, F. & Koch, C. (1978). Towards a neurobiological theory of consciousness. *Seminars in the Neurosciences*, *2*(263-275), 203.

D'Esposito, M. Aguirre, G. K. Zarahn, E. Ballard, D. Shin, R. K. & Lease, J. (1998). Functional MRI studies of spatial and nonspatial working memory. *Brain Research. Cognitive Brain Research*, *7*(1), 1–13.

Damasio, A. R. Damasio, H. & Chui, H. C. (1980). Neglect following damage to frontal lobe or basal ganglia. *Neuropsychologia*, *18*(2), 123–32.

Davis, B. Christie, J. & Rorden, C. (2009a). Temporal order judgments activate temporal parietal junction. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, *29*(10), 3182–8. doi:10.1523/JNEUROSCI.5793-08.2009

Davis, B. Christie, J. & Rorden, C. (2009b). Temporal order judgments activate temporal parietal junction. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, *29*(10), 3182–8. doi:10.1523/JNEUROSCI.5793-08.2009

Desimone, R. & Duncan, J. (1995). Neural mechanisms of selective visual attention. *Annual Review of Neuroscience*, *18*, 193–222.

Di Lollo, V. (2012). Response to Wolfe: feature-binding and object perception. *Trends in Cognitive Sciences*, *16*(6), 308–309. doi:10.1016/j.tics.2012.04.012

Donner, T. H. Kettermann, A. Diesch, E. Ostendorf, F. Villringer, A. & Brandt, S. A. (2002). Visual feature and conjunction searches of equal difficulty engage only partially overlapping frontoparietal networks. *NeuroImage*, *15*(1), 16–25. doi:10.1006/nimg.2001.0951

Dräger, B. Jansen, A. Bruchmann, S. Förster, A. F. Pleger, B. Zwitserlood, P. & Knecht, S. (2004). How does the brain accommodate to increased task difficulty in word finding?

A functional MRI study. *NeuroImage*, *23*(3), 1152–60. doi:10.1016/j.neuroimage.2004.07.005

Driver, J. & Baylis, G. C. (n.d.). Attention and visual object segmentation.

Driver, J. Baylis, G. C. Goodrich, S. J. & Rafal, R. D. (1994a). Axis-based neglect of visual shapes. *Neuropsychologia*, *32*(11), 1353–1356. doi:10.1016/0028-3932(94)00068-9

Driver, J. Baylis, G. C. Goodrich, S. J. & Rafal, R. D. (1994b). Axis-based neglect of visual shapes. *Neuropsychologia*, *32*(11), 1353–1356. doi:10.1016/0028-3932(94)00068-9

Du Boisgueheneuc, F. Levy, R. Volle, E. Seassau, M. Duffau, H. Kinkingnehun, S. … Dubois, B. (2006). Functions of the left superior frontal gyrus in humans: a lesion study. *Brain : A Journal of Neurology*, *129*(Pt 12), 3315–28. doi:10.1093/brain/awl244

Duncan, J. (1984). Selective attention and the organization of visual information. *Journal of Experimental Psychology. General*, *113*(4), 501–17.

Duncan, J. (1984). Selective attention and the organization of visual information. *Journal of Experimental Psychology: General*, *113*(4), 501–517.

Duncan, J. & Humphreys, G. (1992). Beyond the search surface: Visual search and attentional engagement. *Journal of Experimental Psychology: Human Perception and Performance*, *18*(2), 578–588.

Duncan, J. & Owen, A. M. (2000). Common regions of the human frontal lobe recruited by diverse cognitive demands. *Trends in Neurosciences*, *23*(10), 475–483.

Edelman, G. (2006). Consciousness: The Remembered Present. *Annals of the New York Academy of Sciences*, *929*(1), 111–122. doi:10.1111/j.1749-6632.2001.tb05711.x

Egly, R. Driver, J. & Rafal, R. D. (n.d.-a). Shifting visual attention between objects and locations: Evidence from normal and parietal lesion subjects.

Egly, R. Rafal, R. Driver, J. & Starrveveld, Y. (1994). COVERT ORIENTING IN THE SPLIT BRAIN REVEALS HEMISPHERIC SPECIALIZATION FOR OBJECT-BASED ATTENTION. *Psychological Science*, *5*(6), 380–382.

Egner, T. & Hirsch, J. (2005). Cognitive control mechanisms resolve conflict through cortical amplification of task-relevant information. *Nature Neuroscience*, *8*(12), 1784–90. doi:10.1038/nn1594

Elliott, R. & Dolan, R. J. (1998). Activation of Different Anterior Cingulate Foci in Association with Hypothesis Testing and Response Selection. *NeuroImage*, *8*(1), 17–29.

Emmanouil, T. A. Burton, P. & Ro, T. (2013). Unconscious Processing of Unattended Features in Human Visual Cortex. *Journal of Cognitive Neuroscience*, *25*(3), 329–337.

Esterman, M. Verstynen, T. Ivry, R. B. & Robertson, L. C. (2006). Coming unbound: disrupting automatic integration of synesthetic color and graphemes by transcranial magnetic stimulation of the right parietal lobe. *Journal of Cognitive Neuroscience*, *18*(9), 1570–6. doi:10.1162/jocn.2006.18.9.1570

Esterman, M. Verstynen, T. & Robertson, L. C. (2007). Attenuating illusory binding with TMS of the right parietal cortex. *NeuroImage*, *35*(3), 1247–1255.

Farah, M. (1994). Neuropsychological inference with an interactive brain: A critique of the“ locality” assumption. *Behavioral and Brain Sciences*.

FIERRO, B. BRIGHINA, F. PIAZZA, A. OLIVERI, M. & BISIACH, E. (n.d.). Timing of right parietal and frontal cortex activity in visuo-spatial perception : a TMS study in normal individuals. *Neuroreport*, *12*(11), 2605–2607.

Fink, G. (1997). Space-based and object-based visual attention: shared and specific neural domains. *Brain*, *120*(11), 2013–2028. doi:10.1093/brain/120.11.2013

Fischer, J. Spotswood, N. & Whitney, D. (2011). The emergence of perceived position in the visual system. *Journal of Cognitive Neuroscience*, *23*(1), 119–36. doi:10.1162/jocn.2010.21417

Fodor, J. A. & Pylyshyn, Z. W. (1988). Connectionism and cognitive architecture: A critical analysis. *Cognition*, *28*(1), 3–71.

Freedman, D. J. & Assad, J. A. (2006). Experience-dependent representation of visual categories in parietal cortex. *Nature*, *443*(7107), 85–8. doi:10.1038/nature05078

Friedman-Hill, S. R. Robertson, L. C. & Treisman, A. (1995). Parietal contributions to visual feature binding: evidence from a patient with bilateral lesions. *Science (New York, N.Y.)*, *269*(5225), 853–5.

Frings, C. Moeller, B. & Rothermund, K. (2013). Retrieval of event files can be conceptually mediated. *Attention, Perception & Psychophysics*, *75*(4), 700–9.

Fukushima, K. & Yamaguchi, Y. Neural network model of spatial memory, 1 Proceedings of International Conference on Neural Networks ICNN97 548–553 (1997). doi:10.1109/ICNN.1997.611728

Fuster, J. M. (1997). Network memory. *Trends in Neurosciences*, *20*(10), 451–459.

Giesbrecht, B. Woldorff, M. . Song, A. . & Mangun, G. . (2003). Neural mechanisms of top-down control during spatial and feature attention. *NeuroImage*, *19*(3), 496–512. doi:10.1016/S1053-8119(03)00162-9

Goldman-Rakic, P. (1995). Cellular basis of working memory. *Neuron*.

Goodale, M. A. Meenan, J. P. Bülthoff, H. H. Nicolle, D. A. Murphy, K. J. & Racicot, C. I. (2004). Background :, 1–11.

Goodale, M. A. & Milner, A. D. (1992). Separate visual pathways for perception and action. *Trends in Neurosciences*, *15*(1), 20–25.

Goodale, M. A. & Milner, A. D. (1992). Separate visual pathways for perception and action. *Trends in Neurosciences*, *15*(1), 20–5.

Gordon, R. D. & Irwin, D. E. (1996). What's in an object file? Evidence from priming studies. *Perception & Psychophysics*, *58*(8), 1260–77.

Gowen, E. Bradshaw, C. Galpin, A. Lawrence, A. & Poliakoff, E. (2010). Exploring visuomotor priming following biological and non-biological stimuli. *Brain and Cognition*, *74*(3), 288–297.

Graf, M. (2006). Coordinate transformations in object recognition. *Psychological Bulletin*, *132*(6), 920–45. doi:10.1037/0033-2909.132.6.920

Gray, C. M. Engel, A. K. König, P. & Singer, W. (2009). Synchronization of oscillatory neuronal responses in cat striate cortex: Temporal properties. *Visual Neuroscience*, *8*(04), 337. doi:10.1017/S0952523800005071

Grèzes, J. & Decety, J. (2002). Does visual perception of object afford action? Evidence from a neuroimaging study. *Neuropsychologia*, *40*(2), 212–22.

Grill-Spector, K. Kourtzi, Z. & Kanwisher, N. (2001). The lateral occipital complex and its role in object recognition. *Vision Research*, *41*(10), 1409–1422.

GRILLSPECTOR, K. HENSON, R. & MARTIN, A. (2006). Repetition and the brain: neural models of stimulus-specific effects. *Trends in Cognitive Sciences*, *10*(1), 14–23. doi:10.1016/j.tics.2005.11.006

Halford, G. S. Cowan, N. & Andrews, G. (2007). Separating cognitive capacity from knowledge: a new hypothesis. *Trends in Cognitive Sciences*, *11*(6), 236–242.

Hampshire, A. Chamberlain, S. R. Monti, M. M. Duncan, J. & Owen, A. M. (2010). The role of the right inferior frontal gyrus: inhibition and attentional control. *NeuroImage*, *50*(3), 1313–1319.

Hampshire, A. & Owen, A. M. (2006). Fractionating attentional control using event-related fMRI. *Cerebral Cortex (New York, N.Y. : 1991)*, *16*(12), 1679–89. doi:10.1093/cercor/bhj116

Handbook of Neuropsychology: Disorders of visual behavior, Volume 4. (2000) (p. 252). Gulf Professional Publishing.

Hashimoto, R. & Sakai, K. L. (2002). Specialization in the Left Prefrontal Cortex for Sentence Comprehension. *Neuron*, *35*(3), 589–597.

Haxby, J. V, Horwitz, B. Ungerleider, L. G. Maisog, J. M. Pietrini, P. & Grady, C. L. (1994). The functional organization of human extrastriate cortex: a PET-rCBF study of selective attention to faces and locations. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, *14*(11 Pt 1), 6336–53.

Haxby, J. V. Grady, C. L. Horwitz, B. Ungerleider, L. G. Mishkin, M. Carson, R. E. … Rapoport, S. I. (1991). Dissociation of object and spatial visual processing pathways in human extrastriate cortex. *Proceedings of the National Academy of Sciences*, *88*(5), 1621–1625. doi:10.1073/pnas.88.5.1621

Helbig, H. B. Steinwender, J. Graf, M. & Kiefer, M. (2010). Action observation can prime visual object recognition. *Experimental Brain Research*, *200*(3-4), 251–8. doi:10.1007/s00221-009-1953-8

Henderson, J. (1994). Two representational systems in dynamic visual identification. *Journal of Experimental Psychology: General*. Retrieved from http://psycnet.apa.org/psycinfo/1995-08172-001

Henderson, J. & Anes, M. (1994). Roles of object-file review and type priming in visual identification within and across eye fixations. *Journal of Experimental Psychology: …*. Retrieved from http://psycnet.apa.org/journals/xhp/20/4/826/

Heusser, A. C. Awipi, T. & Davachi, L. (2013). The ups and downs of repetition: Modulation of the perirhinal cortex by conceptual repetition predicts priming and long-term memory. *Neuropsychologia*, *51*(12), 2333–2343. doi:10.1016/j.neuropsychologia.2013.04.018

Hirshman, E. Snodgrass, J. G. Mindes, J. & Feenan, K. (1990). Conceptual priming in fragment completion. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *16*(4), 634–647.

Hochstein, S. & Ahissar, M. (2002). View from the Top. *Neuron*, *36*(5), 791–804. Retrieved from http://www.sciencedirect.com/science/article/pii/S0896627302010917

Hoffman, J. E. & Nelson, B. (1981). Spatial selectivity in visual search. *Perception & Psychophysics*, *30*(3), 283–290. doi:10.3758/BF03214284

Hohnsbein, J. & Mateeff, S. (1992). The relation between the velocity of visual motion and the reaction time to motion onset and offset. *Vision Research*, *32*(9), 1789–1791. doi:10.1016/0042-6989(92)90173-G

Holcombe, A. O. (2009). Seeing slow and seeing fast: two limits on perception. *Trends in Cognitive Sciences*, *13*(5), 216–221. Retrieved from http://www.sciencedirect.com/science/article/pii/S1364661309000680

Holcombe, A. O. & Cavanagh, P. (2001). Early binding of feature pairs for visual perception. *Nature Neuroscience*, *4*(2), 127–8.

Hollingworth, A. & Rasmussen, I. P. (n.d.). Binding objects to locations: The relationship between object files and visual working memory.

HOLMES, G. (1919). Disturbances of spatial orientation and visual attention, with loss of stereoscopic vision. A*rchives of neurology and psychiatry*, *1*(4), 385.

Hommel, B. (1998). Automatic stimulus–response translation in dual-task performance. Journal *of Experimental Psychology: Human Perception and*

Hommel, B. (1998). Event Files: Evidence for Automatic Integration of Stimulus-Response Episodes. *Visual Cognition*, *5*(1-2), 183–216.

Hommel, B. (2002). Responding to object files: automatic integration of spatial information revealed by stimulus-response compatibility effects. *The Quarterly Journal of Experimental Psychology. A, Human Experimental Psychology*, *55*(2), 567–80.

Hommel, B. (2004a). Event files: Feature binding in and across perception and action. *Trends in Cognitive Sciences*.

Hommel, B. (2004b). Event files: feature binding in and across perception and action. *Trends in Cognitive Sciences*, *8*(11), 494–500.

Hommel, B. (2007a). Feature integration across perception and action: Event files affect response choice. *Psychological Research*, *71*(1), 42–63.

Hommel, B. (2007b). Feature integration across perception and action: event files affect response choice. *Psychological Research*, *71*(1), 42–63.

Hommel, B. & Colzato, L. (2004). Visual attention and the temporal dynamics of feature integration. *Visual Cognition*, *11*(4), 483–521.

Hommel, B. & Colzato, L. S. (2009). When an object is more than a binding of its features: Evidence for two mechanisms of visual feature integration. *Visual Cognition*, *17*(1-2), 120–140.

Hommel, B. Proctor, R. W. & Vu, K.-P. L. (2004). A feature-integration account of sequential effects in the Simon task. *Psychological Research*, *68*(1), 1–17.

Honey, G. D. Bullmore, E. T. & Sharma, T. (2000). Prolonged Reaction Time to a Verbal Working Memory Task Predicts Increased Power of Posterior Parietal Cortical Activation. *NeuroImage*, *12*(5), 495–503.

Hong, S. W. & Shevell, S. K. (2006). Resolution of binocular rivalry: Perceptual misbinding of color. *Visual Neuroscience*, *23*(3-4), 561–566.

Huang, Y. & Rothwell, J. (2007). *Transcranial Brain Stimulation for Treatment of Psychiatric Disorders*. (M. A. Marcolin & F. Padberg, Eds.) (pp. 187–203). Basel: KARGER.

Humphrey, G. K. & Goodale, M. A. (1998). Probing Unconscious Visual Processing with the McCollough Effect. *Consciousness and Cognition*, *7*(3), 494–519.

Humphreys, G. W. Riddoch, M. J. Nys, G. & Heinke, D. (2002). Transient binding by time: Neuropsychological evidence from anti-extinction. *Cognitive Neuropsychology*, *19*(4), 361–80.

Husain, M. & Nachev, P. (2007). Space and the parietal cortex. *Trends in Cognitive Sciences*, *11*(1), 30–36.

Hutton, C. Bork, A. Josephs, O. Deichmann, R. Ashburner, J. & Turner, R. (2002). Image distortion correction in fMRI: A quantitative evaluation. *NeuroImage*, *16*(1), 217–40.

Hyun, J.-S. Woodman, G. F. & Luck, S. J. (2009). The Role of Attention in the Binding of Surface Features to Locations. *Visual Cognition*, *17*(1-2), 10–24.

Jager, G. (2003). On the hemispheric specialization for categorical and coordinate spatial relations: a review of the current evidence. *Neuropsychologia*, *41*(4), 504–515.

Jager, G. & Postma, A. (2003). On the hemispheric specialization for categorical and coordinate spatial relations: a review of the current evidence. *Neuropsychologia*, *41*(4), 504–15.

James, T. W. Culham, J. Humphrey, G. K. Milner, A. D. & Goodale, M. A. (2003). Ventral occipital lesions impair object recognition but not object-directed grasping: an fMRI study. *Brain : A Journal of Neurology*, *126*(Pt 11), 2463–75. doi:10.1093/brain/awg248

Jaswal, S. (2012). The importance of being relevant. *Frontiers in Psychology*, *3*, 309. doi:10.3389/fpsyg.2012.00309

Jonides, J. (1981). Voluntary versus automatic control over the mind’s eye's movement. *Attention and Performance IX*.

Kaas, J. H. & Lyon, D. C. (2001). *Vision: From Neurons to Cognition* (Vol. 134). Elsevier.

Kahneman, D. & Treisman, A. (1984). Changing views of attention and automaticity. *Varieties of Attention*.

Kahneman, D. Treisman, A. & Gibbs, B. J. (1992a). The reviewing of object files: Object-specific integration of information. *Cognitive Psychology*, *24*(2), 175–219.

Kahneman, D. Treisman, A. & Gibbs, B. J. (1992b). The reviewing of object files: Object-specific integration of information. *Cognitive Psychology*, *24*(2), 175–219.

Kahneman, D. Treisman, A. & Gibbs, B. J. (1992). The reviewing of object files: object-specific integration of information. *Cognitive Psychology*, *24*(2), 175–219.

Kang, P. & Shevell, S. (2010). Does color misbind to achromatic regions or chromatically similar regions? *Journal of Vision*, *9*(8), 302–302.

Kanwisher, E. W. N. (1998). Implicit but not Explicit Feature Binding in a Balint's Patient. *Visual Cognition*, *5*(1-2), 157–181.

Kanwisher, N. (1991). Repetition blindness and illusory conjunctions: errors in binding visual types with visual tokens. *Journal of Experimental Psychology. Human Perception and Performance*, *17*(2), 404–421.

Kanwisher, N. (2010). Functional specificity in the human brain: a window into the functional architecture of the mind. *Proceedings of the National Academy of Sciences of the United States of America*, *107*(25), 11163–70.

Kanwisher, N. Chun, M. M. McDermott, J. & Ledden, P. J. (1996). Functional imaging of human visual recognition. *Cognitive Brain Research*, *5*(1-2), 55–67.

Kanwisher, N. McDermott, J. & Chun, M. M. (1997). The fusiform face area: a module in human extrastriate cortex specialized for face perception. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, *17*(11), 4302–11.

Kanwisher, N. & Wojciulik, E. (2000). Visual attention: insights from brain imaging. *Nature Reviews. Neuroscience*, *1*(2), 91–100.

Kastner, S. Pinsk, M. A. De Weerd, P. Desimone, R. & Ungerleider, L. G. (1999). Increased Activity in Human Visual Cortex during Directed Attention in the Absence of Visual Stimulation. *Neuron*, *22*(4), 751–761.

Kastner, S. Pinsk, M. A. De Weerd, P. Desimone, R. & Ungerleider, L. G. (1999). Increased activity in human visual cortex during directed attention in the absence of visual stimulation. *Neuron*, *22*(4), 751–61.

Keizer, A. W. Colzato, L. S. & Hommel, B. (2008). Integrating faces, houses, motion, and action: spontaneous binding across ventral and dorsal processing streams. *Acta Psychologica*, *127*(1), 177–85.

Keizer, A. W. Nieuwenhuis, S. Colzato, L. S. Teeuwisse, W. Rombouts, S. A. & Hommel, B. (2008). When moving faces activate the house area: an fMRI study of object-file retrieval. *Behavioral and Brain Functions : BBF*, *4*, 50.

Kerns, J. G. Cohen, J. D. MacDonald, A. W. Cho, R. Y. Stenger, V. A. & Carter, C. S. (2004). Anterior cingulate conflict monitoring and adjustments in control. *Science (New York, N.Y.)*, *303*(5660), 1023–6.

Koch, K. McLean, J. Segev, R. Freed, M. A. Berry, M. J. Balasubramanian, V. & Sterling, P. (2006). How much the eye tells the brain. *Current Biology : CB*, *16*(14), 1428–34.

Kosslyn, S. M. Koenig, O. Barrett, A. Cave, C. B. Tang, J. & Gabrieli, J. D. (1989). Evidence for two types of spatial representations: hemispheric specialization for categorical and coordinate relations. *Journal of Experimental Psychology. Human Perception and Performance*, *15*(4), 723–35.

Kosslyn, S. M. Koenig, O. Barrett, A. Cave, C. B. Tang, J. & Gabrieli, J. D. E. (n.d.). Evidence for two types of spatial representations: Hemispheric specialization for categorical and coordinate relations.

Kramer, A. F. Weber, T. A. & Watson, S. E. (1997). Object-based attentional selection—Grouped arrays or spatially invariant representations?: Comment on Vecera and Farah (1994). *Journal of Experimental Psychology: General*, *126*(1), 3–13.

Kühn, S. Keizer, A. W. Colzato, L. S. Rombouts, S. A. R. B. & Hommel, B. (2010). The Neural Underpinnings of Event-file Management: Evidence for Stimulus-induced Activation of and Competition among Stimulus–Response Bindings.

LaBerge, D. & Buchsbaum, M. S. (1990). Positron emission tomographic measurements of pulvinar activity during an attention task. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, *10*(2), 613–9.

Lamme, V. A. F. & Roelfsema, P. R. (2000). The distinct modes of vision offered by feedforward and recurrent processing. *Trends in Neurosciences*, *23*(11), 571–579.

Lamy, D. & Tsal, Y. (n.d.). Object features, object locations, and object files: Which does selective attention activate and when?

Lamy, D. & Tsal, Y. (2001). On the status of location in visual attention. *European Journal of Cognitive Psychology*, *13*(3), 305–342.

LaRock, E. (2007). Disambiguation, Binding, and the Unity of Visual Consciousness. *Theory & Psychology*, *17*(6), 747–777.

Lavie, N. (1995). Perceptual load as a necessary condition for selective attention. *Journal of Experimental Psychology. Human Perception and Performance*, *21*(3), 451–68.

Lavie, N. (2005). Distracted and confused?: Selective attention under load. *Trends in Cognitive Sciences*, *9*(2), 75–82.

Lavie, N. & Driver, J. (1996). On the spatial extent of attention in object-based visual selection. *Perception & Psychophysics*, *58*(8), 1238–1251.

Lavie, N. Hirst, A. de Fockert, J. & Viding, E. (2004, September 1). Load theory of selective attention and cognitive control. *Journal of experimental psychological gen*. amer psychological assoc.

Leslie, A. M. Xu, F. Tremoulet, P. D. & Scholl, B. J. (1998). Indexing and the object concept: developing `what’ and `where' systems. *Trends in Cognitive Sciences*, *2*(1), 10–18.

Linares, D. & López-Moliner, J. (2006). Perceptual asynchrony between color and motion with a single direction change. *Journal of Vision*, *6*(9), 974–981.

Logothetis, N. K. (2008). What we can do and what we cannot do with fMRI. *Nature*, *453*(7197), 869–878.

Lollo, V. Di, Enns, J. & Rensink, R. (2000). Competition for consciousness among visual events: the psychophysics of reentrant visual processes. *Journal of Experimental.*

Lopez-Moliner, J. & Linares, D. (2010). Perceived duration is shortened after motion direction changes. *Journal of Vision*, *7*(9), 377–377.

Love, T. & Swinney, D. (1996). Coreference processing and levels of analysis in object-relative constructions; Demonstration of antecedent reactivation with the cross-modal priming paradigm. *Journal of Psycholinguistic Research*, *25*(1), 5–24.

Luck, S. J. & Vogel, E. K. (1997). The capacity of visual working memory for features and conjunctions. *Nature*, *390*(6657), 279–81.

MacLeod, C. M. (1991). Half a century of research on the Stroop effect: an integrative review. *Psychological Bulletin*, *109*(2), 163–203.

Malsburg C von Der. (1981). *The correlation theory of brain function.* (p. Internal Report 81–2). Göttingen.

Mao, L. Zhou, B. Zhou, W. & Han, S. (2007). Neural correlates of covert orienting of visual spatial attention along vertical and horizontal dimensions. *Brain Research*, *1136*(1), 142–53.

Marois, R. Chun, M. M. & Gore, J. C. (2000). Neural Correlates of the Attentional Blink. *Neuron*, *28*(1), 299–308.

Mars, R. B. Klein, M. C. Neubert, F.-X. Olivier, E. Buch, E. R. Boorman, E. D. & Rushworth, M. F. S. (2009). Short-latency influence of medial frontal cortex on primary motor cortex during action selection under conflict. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, *29*(21), 6926–31.

Maunsell, J. H. R. & Treue, S. (2006). Feature-based attention in visual cortex. *Trends in Neurosciences*, *29*(6), 317–22.

Mayer, K. M. & Vuong, Q. C. (2012). The influence of unattended features on object processing depends on task demand. *Vision Research*, *56*, 20–7.

McClelland, A. G. R. & Pring, L. (1991). An investigation of cross-modality effects in implicit and explicit memory. *The Quarterly Journal of Experimental Psychology Section A*, *43*(1), 19–33.

McGraw, P. V, Walsh, V. & Barrett, B. T. (2004). Motion-sensitive neurones in V5/MT modulate perceived spatial position. *Current Biology : CB*, *14*(12), 1090–3.

Melcher, D. Papathomas, T. V, & Vidnyánszky, Z. (2005a). Implicit attentional selection of bound visual features. *Neuron*, *46*(5), 723–9.

Melcher, D. Papathomas, T. V, & Vidnyánszky, Z. (2005b). Implicit attentional selection of bound visual features. *Neuron*, *46*(5), 723–9.

Melcher, D. Papathomas, T. V. & Vidnyánszky, Z. (2005c). Implicit attentional selection of bound visual features. *Neuron*, *46*(5), 723–9.

Mesulam, M. M. (1981). A cortical network for directed attention and unilateral neglect. *Annals of Neurology*, *10*(4), 309–25.

Mesulam, M. M. (1999a). Spatial attention and neglect: parietal, frontal and cingulate contributions to the mental representation and attentional targeting of salient extrapersonal events. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *354*(1387), 1325–46.

Mesulam, M. M. (1999b). Spatial attention and neglect: parietal, frontal and cingulate contributions to the mental representation and attentional targeting of salient extrapersonal events. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *354*(1387), 1325–46.

milesian: Superior view of the brain revealing... (n.d.).

Mishkin, M. Ungerleider, L. G. & Macko, K. A. (1983). Object vision and spatial vision: two cortical pathways. *Trends in Neurosciences*, *6*, 414–417.

Mitroff, S. R. & Alvarez, G. A. (2007). Space and time, not surface features, guide object persistence. *Psychonomic Bulletin & Review*, *14*(6), 1199–1204.

Mitroff, S. R. & Scholl, B. J. (2005). Forming and updating object representations without awareness: evidence from motion-induced blindness. *Vision Research*, *45*(8), 961–7.

Mitroff, S. R. Scholl, B. J. & Wynn, K. (2005). The relationship between object files and conscious perception. *Cognition*, *96*(1), 67–92.

Mitroff, S. Scholl, B. & Noles, N. (2007). Object files can be purely episodic.

Motter, B. (1994). Neural correlates of attentive selection for color or luminance in extrastriate area V4. *The Journal of Neuroscience*.

Mountcastle, V. Motter, B. Steinmetz, M. & Sestokas, A. (1987). Common and differential effects of attentive fixation on the excitability of parietal and prestriate (V4) cortical visual neurons in the macaque monkey. *J. Neurosci. 7*(7), 2239–2255.

Muggleton, N. G. Chen, C.-Y. Tzeng, O. J. L. Hung, D. L. & Juan, C.-H. (2010). Inhibitory control and the frontal eye fields. *Journal of Cognitive Neuroscience*, *22*(12), 2804–12.

Müller, M. M. Andersen, S. Trujillo, N. J. Valdés-Sosa, P. Malinowski, P. & Hillyard, S. a. (2006). Feature-selective attention enhances color signals in early visual areas of the human brain. *Proceedings of the National Academy of Sciences of the United States of America*, *103*(38), 14250–4.

Navarrete, E. & Costa, A. (2005). Phonological activation of ignored pictures: Further evidence for a cascade model of lexical access☆. *Journal of Memory and Language*, *53*(3), 359–377.

Nobre, A. (1997). Functional localization of the system for visuospatial attention using positron emission tomography. *Brain*, *120*(3), 515–533.

Nobre, A. C. Coull, J. T. Walsh, V. & Frith, C. D. (2003). Brain Activations during Visual Search: Contributions of Search Efficiency versus Feature Binding. *NeuroImage*, *18*(1), 91–103.

Nobre, A. C. Coull, J. T. Walsh, V. & Frith, C. D. (2003). Brain activations during visual search: contributions of search efficiency versus feature binding. *NeuroImage*, *18*(1), 91–103.

Nobre, A. C. Sebestyen, G. N. Gitelman, D. R. Mesulam, M. M. Frackowiak, R. S. & Frith, C. D. (1997). Functional localization of the system for visuospatial attention using positron emission tomography. *Brain : A Journal of Neurology*, *120, Pt 3*, 515–33.

O'Craven, K. M. Downing, P. E. & Kanwisher, N. (1999a). fMRI evidence for objects as the units of attentional selection. *Nature*, *401*(6753), 584–7.

O'Craven, K. M. Downing, P. E. & Kanwisher, N. (1999b). fMRI evidence for objects as the units of attentional selection. *Nature*, *401*(6753), 584–7.

O'Craven, K. M. & Kanwisher, N. (2000). Mental imagery of faces and places activates corresponding stiimulus-specific brain regions. *Journal of Cognitive Neuroscience*, *12*(6), 1013–23.

O'Craven, K. M. & Kanwisher, N. (2000a). Mental Imagery of Faces and Places Activates Corresponding Stimulus-Specific Brain Regions. *Journal of Cognitive Neuroscience*, *12*(6), 1013–1023.

O'Craven, K. M. & Kanwisher, N. (2000b). Mental Imagery of Faces and Places Activates Corresponding Stimulus-Specific Brain Regions. *Journal of Cognitive Neuroscience*, *12*(6), 1013–1023.

O'Craven, K. M. Rosen, B. R. Kwong, K. K. Treisman, A. & Savoy, R. L. (1997). Voluntary Attention Modulates fMRI Activity in Human MT–MST. *Neuron*, *18*(4), 591–598.

Oberman, L. Edwards, D. Eldaief, M. & Pascual-Leone, A. (2011). Safety of theta burst transcranial magnetic stimulation: a systematic review of the literature. *Journal of Clinical Neurophysiology : Official Publication of the American Electroencephalographic Society*, *28*(1), 67–74.

Olson, I. R. Moore, K. S. Stark, M. & Chatterjee, A. (2006). Visual working memory is impaired when the medial temporal lobe is damaged. *Journal of Cognitive Neuroscience*, *18*(7), 1087–97.

Ong, W. S. Hooshvar, N. Zhang, M. & Bisley, J. W. (2009). Psychophysical evidence for spatiotopic processing in area MT in a short-term memory for motion task. *Journal of Neurophysiology*, *102*(4), 2435–40.

Parkkonen, L. Andersson, J. Hämäläinen, M. & Hari, R. (2008). Early visual brain areas reflect the percept of an ambiguous scene. *Proceedings of the National Academy of Sciences of the United States of America*, *105*(51), 20500–4.

Parks, R. W. & Levine, D. S. (1998). Attention and neural networks. In *Fundamentals of neural network modeling Neuropsychology and cognitive neuroscience* (p. 61). The MIT Press.

Petersen, S. E. Corbetta, M. Miezin, F. M. & Shulman, G. L. (1994). PET studies of parietal involvement in spatial attention: comparison of different task types. *Canadian Journal of Experimental Psychology, Revue Canadienne de Psychologie Expérimentale*, *48*(2), 319–38.

Piekema, C. Rijpkema, M. Fernández, G. & Kessels, R. P. C. (2010). Dissociating the neural correlates of intra-item and inter-item working-memory binding. *PloS One*, *5*(4), e10214.

Pöppel, E. (1997). A hierarchical model of temporal perception. *Trends in Cognitive Sciences*, *1*(2), 56–61.

Posner, M. I. (1980). Orienting of attention. *Quarterly Journal of Experimental Psychology*, *32*(1), 3–25.

Postle, B. R. Berger, J. S. Taich, A. M. & D'Esposito, M. (2000). Activity in human frontal cortex associated with spatial working memory and saccadic behavior. *Journal of Cognitive Neuroscience*, *12 Suppl 2*, 2–14.

Prabhakaran, V. Narayanan, K. Zhao, Z. & Gabrieli, J. D. (2000). Integration of diverse information in working memory within the frontal lobe. *Nature Neuroscience*, *3*(1), 85–90.

Prinzmetal, W. Presti, D. E. & Posner, M. I. (n.d.). Does attention affect visual feature integration?

Ranganath, C. Johnson, M. K. & D'Esposito, M. (2003). Prefrontal activity associated with working memory and episodic long-term memory. *Neuropsychologia*, *41*(3), 378–389.

Rao, S. M. Mayer, A. R. & Harrington, D. L. (2001). The evolution of brain activation during temporal processing. *Nature Neuroscience*, *4*(3), 317–23.

Reales, J. M. & Ballesteros, S. (1999). Implicit and explicit memory for visual and haptic objects: Cross-modal priming depends on structural descriptions.

Rees, G. (1997). Two Modulatory Effects of Attention That Mediate Object Categorization in Human Cortex. *Science*, *275*(5301), 835–838.

Reis, J. Swayne, O. B. Vandermeeren, Y. Camus, M. Dimyan, M. A. Harris-Love, M. Cohen, L. G. (2008). Contribution of transcranial magnetic stimulation to the understanding of cortical mechanisms involved in motor control. *The Journal of Physiology*, *586*(2), 325–51. doi:10.1113/jphysiol.2007.144824

Rizzolatti, G. & Camarda, R. (1987). Neural circuits for spatial attention and unilateral neglect. In M. Jeannerod (Ed.), *Neurophysiological and Neuropsychological Aspects of Spatial Neglect* (pp. 289–313). North-Holland.

Ro, T. Friggel, A. & Lavie, N. (2007). Attentional biases for faces and body parts. *Visual Cognition*, *15*(3), 322–348.

Robertson, I. H. Mattingley, J. B. Rorden, C. & Driver, J. (1998). Phasic alerting of neglect patients overcomes their spatial deficit in visual awareness. *Nature*, *395*(6698), 169–72.

Robertson, L. C. (2003a). Binding, spatial attention and perceptual awareness. *Nature Reviews. Neuroscience*, *4*(2), 93–102.

Robertson, L. C. (2003b). *Space, Objects, Minds and Brains (Google eBook)* (Vol. 2003, p. 272). Psychology Press.

Robertson, L. & Treisman, A. (1995a). Parietal contributions to visual feature binding: evidence from a patient with bilateral lesions. *Science*, *269*(5225), 853–855. d

Robertson, L. & Treisman, A. (1995b). Parietal contributions to visual feature binding: evidence from a patient with bilateral lesions. *Science*, *269*(5225), 853–855. doi:10.1126/science.7638604

Robertson, L. Treisman, A. Friedman-Hill, S. & Grabowecky, M. (1997). The Interaction of Spatial and Object Pathways: Evidence from Balint's Syndrome. *Journal of Cognitive Neuroscience*, *9*(3), 295–317.

Roe, A. W. Chelazzi, L. Connor, C. E. Conway, B. R. Fujita, I. Gallant, J. L. … Vanduffel, W. (2012). Toward a unified theory of visual area V4. *Neuron*, *74*(1), 12–29.

Rorden, C. & Brett, M. (2000). Stereotaxic display of brain lesions. *Behavioural Neurology*, *12*(4/2000), 191–200.

Rorden, C. Mattingley, J. B. Karnath, H. O. & Driver, J. (1997). Visual extinction and prior entry: impaired perception of temporal order with intact motion perception after unilateral parietal damage. *Neuropsychologia*, *35*(4), 421–33.

Rossion, B. & Gauthier, I. (n.d.). How does the brain process upright and inverted faces?

Rossion, B. & Gauthier, I. (2002). How Does the Brain Process Upright and Inverted Faces? *Behavioral and Cognitive Neuroscience Reviews*, *1*(1), 63–75.

Saenz, M. Buracas, G. T. & Boynton, G. M. (2002). Global effects of feature-based attention in human visual cortex. *Nature Neuroscience*, *5*(7), 631–2.

Sagiv, N. Heer, J. & Robertson, L. (2006). Does Binding of Synesthetic Color to the Evoking Grapheme Require Attention? *Cortex*, *42*(2), 232–242.

Saiki, J. (2003). Spatiotemporal characteristics of dynamic feature binding in visual working memory. *Vision Research*, *43*(20), 2107–2123.

Sakai, K. Rowe, J. B. & Passingham, R. E. (2002). Active maintenance in prefrontal area 46 creates distractor-resistant memory. *Nature Neuroscience*, *5*(5), 479–84. doi:10.1038/nn846

Salinas, E. & Sejnowski, T. J. (2001). Gain modulation in the central nervous system: where behavior, neurophysiology, and computation meet. *The Neuroscientist : A Review Journal Bringing Neurobiology, Neurology and Psychiatry*, *7*(5), 430–40.

Schacter, D. L. (1992). Priming and multiple memory systems: perceptual mechanisms of implicit memory. *Journal of Cognitive Neuroscience*, *4*(3), 244–56.

Schenkluhn, B. Ruff, C. C. Heinen, K. & Chambers, C. D. (2008, October 1). Parietal stimulation decouples spatial and feature-based attention. *Journal of Neuroscience*. Society for Neuroscience.

Schoenfeld, M. A. Hopf, J.-M. Merkel, C. Heinze, H.-J. & Hillyard, S. A. (2014a). Object-based attention involves the sequential activation of feature-specific cortical modules. *Nature Neuroscience*, *17*(4), 619–24.

Schoenfeld, M. A. Hopf, J.-M. Merkel, C. Heinze, H.-J. & Hillyard, S. A. (2014b). Object-based attention involves the sequential activation of feature-specific cortical modules. *Nature Neuroscience*, *17*(4), 619–24.

Schoenfeld, M. A. Tempelmann, C. Martinez, A. Hopf, J.-M. Sattler, C. Heinze, H.-J. & Hillyard, S. A. (2003). Dynamics of feature binding during object-selective attention. *Proceedings of the National Academy of Sciences of the United States of America*, *100*(20), 11806–11.

Schulte, T. Müller-Oehring, E. M. Vinco, S. Hoeft, F. Pfefferbaum, A. & Sullivan, E. V. (2009). Double dissociation between action-driven and perception-driven conflict resolution invoking anterior versus posterior brain systems. *NeuroImage*, *48*(2), 381–90. doi:10.1016/j.neuroimage.2009.06.058

Serences, J. T. Schwarzbach, J. Courtney, S. M. Golay, X. & Yantis, S. (2004). Control of object-based attention in human cortex. *Cerebral Cortex (New York, N.Y. : 1991)*, *14*(12), 1346–57.

Sereno, M. I. Pitzalis, S. & Martinez, A. (2001a). Mapping of contralateral space in retinotopic coordinates by a parietal cortical area in humans. *Science (New York, N.Y.)*, *294*(5545), 1350–4.

Sereno, M. I. Pitzalis, S. & Martinez, A. (2001b). Mapping of contralateral space in retinotopic coordinates by a parietal cortical area in humans. *Science (New York, N.Y.)*, *294*(5545), 1350–4. doi:10.1126/science.1063695

Seymour, K. Clifford, C. W. G. Logothetis, N. K. & Bartels, A. (2009a). The coding of color, motion, and their conjunction in the human visual cortex. *Current Biology : CB*, *19*(3), 177–83.

Seymour, K. Clifford, C. W. G. Logothetis, N. K. & Bartels, A. (2009b). The coding of color, motion, and their conjunction in the human visual cortex. *Current Biology : CB*, *19*(3), 177–83.

Seymour, K. Clifford, C. W. G. Logothetis, N. K. & Bartels, A. (2010). Coding and binding of color and form in visual cortex. *Cerebral Cortex (New York, N.Y. : 1991)*, *20*(8), 1946–54.

Shafritz, K. M. Gore, J. C. & Marois, R. (2002). The role of the parietal cortex in visual feature binding. *Proceedings of the National Academy of Sciences*, *99*(16), 10917–10922.

Shafritz, K. M. Gore, J. C. & Marois, R. (2002). The role of the parietal cortex in visual feature binding. *Proceedings of the National Academy of Sciences of the United States of America*, *99*(16), 10917–22.

Shevell, S. K. St Clair, R. & Hong, S. W. (2008). Misbinding of color to form in afterimages. *Visual Neuroscience*, *25*(3), 355–360.

Shipp, S. Adams, D. L. Moutoussis, K. & Zeki, S. (2009). Feature binding in the feedback layers of area V2. *Cerebral Cortex (New York, N.Y. : 1991)*, *19*(10), 2230–9.

Shipp, S. & Zeki, S. (1995). Segregation and convergence of specialised pathways in macaque monkey visual cortex. *Journal of Anatomy*, *187 (Pt 3*, 547–62.

Shulman, L. & Petersen, E. (1991). Selective and Divided Attention during Visual Discriminations Shape , Color , and Speed : Functional Anatomy by Positron Emission Tomography, (August), 2393–2402.

Siebner, H. R. & Rothwell, J. (2003). Transcranial magnetic stimulation: new insights into representational cortical plasticity. *Experimental Brain Research*, *148*(1), 1–16.

Singer, W. & Gray, C. M. (1995a). Visual feature integration and the temporal correlation hypothesis. *Annual Review of Neuroscience*, *18*, 555–86.

Singer, W. & Gray, C. M. (1995b). Visual feature integration and the temporal correlation hypothesis. *Annual Review of Neuroscience*, *18*, 555–86.

Sinnett, S. Juncadella, M. Rafal, R. Azañón, E. & Soto-Faraco, S. (2007). A dissociation between visual and auditory hemi-inattention: Evidence from temporal order judgements. *Neuropsychologia*, *45*(3), 552–60.

Sirigu, A. Duhamel, J.-R. Cant, J. S. Westwood, D. A. Valyear, K. F. & Goodale, M. A. (2005). No evidence for visuomotor priming in a visually guided action task. *Neuropsychologia*, *43*(2), 216–226.

Slagter, H. A. Giesbrecht, B. Kok, A. Weissman, D. H. Kenemans, J. L. Woldorff, M. G. & Mangun, G. R. (2007). fMRI evidence for both generalized and specialized components of attentional control. *Brain Research*, *1177*, 90–102.

Sligte, I. G. Scholte, H. S. & Lamme, V. A. F. (2008). Are there multiple visual short-term memory stores? *PloS One*, *3*(2), e1699.

Slotnick, S. D. & Moo, L. R. (2006). Prefrontal cortex hemispheric specialization for categorical and coordinate visual spatial memory. *Neuropsychologia*, *44*(9), 1560–8.

Smith, F. W. & Goodale, M. A. (2014). Decoding Visual Object Categories in Early Somatosensory Cortex. *Cerebral Cortex (New York, N.Y. : 1991)*.

Smith, S. M. (2002). Fast robust automated brain extraction. *Human Brain Mapping*, *17*(3), 143–55.

Smith, D. V, Clithero, J. A. Rorden, C. & Karnath, H.-O. (2013). Decoding the anatomical network of spatial attention. *Proceedings of the National Academy of Sciences of the United States of America*, *110*(4), 1518–23.

Snyder, A. C. Fiebelkorn, I. C. & Foxe, J. J. (2012). Pitting binding against selection--electrophysiological measures of feature-based attention are attenuated by Gestalt object grouping. *The European Journal of Neuroscience*, *35*(6), 960–7.

Snyder, J. J. & Chatterjee, A. (2004a). Spatial-temporal anisometries following right parietal damage. *Neuropsychologia*, *42*(12), 1703–1708.

Snyder, J. J. & Chatterjee, A. (2004b). Spatial-temporal anisometries following right parietal damage. *Neuropsychologia*, *42*(12), 1703–8.

Sohn, W. Papathomas, T. V. Blaser, E. & Vidnyánszky, Z. (2004). Object-based cross-feature attentional modulation from color to motion. In *Vision Research* (Vol. 44, pp. 1437–1443).

Sterzer, P. & Kleinschmidt, A. (2005). A neural signature of colour and luminance correspondence in bistable apparent motion. *The European Journal of Neuroscience*, *21*(11), 3097–106.

Sterzer, P. Kleinschmidt, A. & Rees, G. (2009). The neural bases of multistable perception. *Trends in Cognitive Sciences*, *13*(7), 310–8.

Swick, D. Ashley, V. & Turken, U. (2011). Are the neural correlates of stopping and not going identical? Quantitative meta-analysis of two response inhibition tasks. *NeuroImage*, *56*(3), 1655–65.

Terjung, R. (Ed.). (2011). *Comprehensive Physiology*. Hoboken, NJ, USA: John Wiley & Sons, Inc.

The Mendeley Support Team. (2011). Getting Started with Mendeley. *Mendeley Desktop*. London: Mendeley Ltd.

The Neural Basis of Multisensory Spatial and Feature-Based Attention in Vision and Somatosensation. (n.d.).

Theeuwes, J. Mathôt, S. & Kingstone, A. (2010). Object-based eye movements: the eyes prefer to stay within the same object. *Attention, Perception & Psychophysics*, *72*(3), 597–601.

Tipper, S. P. & Driver, J. (1988). Negative priming between pictures and words in a selective attention task: Evidence for semantic processing of ignored stimuli. *Memory & Cognition*, *16*(1), 64–70. doi:10.3758/BF03197746

Tipper, S. P. Weaver, B. Jerreat, L. M. & Burak, A. L. (n.d.). Object-based and environment-based inhibition of return of visual attention. *Journal of Experimental Psychology. Human Perception and Performance*, *20*(3), 478–499.

Todd, J. J. & Marois, R. (2005). Posterior parietal cortex activity predicts individual differences in visual short-term memory capacity. *Cognitive, Affective & Behavioral Neuroscience*, *5*(2), 144–55.

Tootell, R. B. H. Reppas, J. B. Kwong, K. K. Malach, R. Belliveau, J. W. Brady, T. J. & Rosen, B. R. (1994). Coding of motion and color in human cortical area MT/V5 (p. 690).

Toth, L. J. & Assad, J. A. (2002). Dynamic coding of behaviourally relevant stimuli in parietal cortex. *Nature*, *415*(6868), 165–8.

Treisman, A. (1982). Perceptual grouping and attention in visual search for features and for objects. *Journal of Experimental Psychology. Human Perception and Performance*, *8*(2), 194–214.

Treisman, A. (1985). Preattentive processing in vision. *Computer Vision, Graphics, and Image Processing*, *31*(2), 156–177.

Treisman, A. (1988). Features and objects: The fourteenth bartlett memorial lecture. *The Quarterly Journal of Experimental Psychology Section A*, *40*(2), 201–237.

Treisman, A. (1994). Visual attention and the perception of features and objects. *Canadian Psychology/Psychologie Canadienne*.

Treisman, A. (1996). The binding problem. *Current Opinion in Neurobiology*, *6*(2), 171–178.

Treisman, A. (1998). Feature binding, attention and object perception. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *353*(1373), 1295–306.

Treisman, A. (2006). How the deployment of attention determines what we see. *Visual Cognition*, *14*(4-8), 411–443.

Treisman, A. Kahneman, D. & Burkell, J. (1983). Perceptual objects and the cost of filtering. *Perception & Psychophysics*, *33*(6), 527–532.

Treisman, A. M. & Gelade, G. (1980). A feature-integration theory of attention. *Cognitive Psychology*, *12*(1), 97–136.

Treisman, A. M. & Gelade, G. (1980). A feature-integration theory of attention. *Cognitive Psychology*, *12*(1), 97–136.

Treisman, A. & Paterson, R. (1984). Emergent features, attention, and object perception. *Journal of Experimental Psychology. Human Perception and Performance*, *10*(1), 12–31.

Treisman, A. & Schmidt, H. (1982). Illusory conjunctions in the perception of objects. *Cognitive Psychology*, *14*(1), 107–141. doi:10.1016/0010-0285(82)90006-8

Treisman, A. & Schmidt, H. (1982). Illusory conjunctions in the perception of objects. *Cognitive Psychology*, *14*(1), 107–141.

Treisman, A. & Zhang, W. (2006). Location and binding in visual working memory. *Memory & Cognition*, *34*(8), 1704–19.

Treue, S. & Martínez Trujillo, J. C. (1999). Feature-based attention influences motion processing gain in macaque visual cortex. *Nature*, *399*(6736), 575–9.

Trojano, L. Grossi, D. Linden, D. E. . Formisano, E. Goebel, R. Cirillo, S. … Di Salle, F. (2002). Coordinate and categorical judgements in spatial imagery. An fMRI study. *Neuropsychologia*, *40*(10), 1666–1674.

Turella, L. Tubaldi, F. Erb, M. Grodd, W. & Castiello, U. (2012). Object presence modulates activity within the somatosensory component of the action observation network. *Cerebral Cortex (New York, N.Y. : 1991)*, *22*(3), 668–79.

Tutorials in Visual Cognition. (2011) (p. 405). Routledge.

Ungerleider, L. G. Galkin, T. W. & Mishkin, M. (1983). Visuotopic organization of projections from striate cortex to inferior and lateral pulvinar in rhesus monkey. *The Journal of Comparative Neurology*, *217*(2), 137–57. doi:10.1002/cne.902170203

Ungerleider, L. & Haxby, J. (1994). “What”and “where”in the human brain. *Current Opinion in Neurobiology*, *4*(2), 157–165. Retrieved from http://www.sciencedirect.com/science/article/pii/0959438894900663

Ungerleider, L. & Miskin, M. (1982a). Two cortical visual systems In DJ Engle, MA Goodale, & RJ Mansfield (Eds.) Analysis of visual behavior, 549-586.

Ungerleider, L. & Miskin, M. (1982b). Two visual pathways. *Analysis of Visual Behavior*.

Vaina, L. M. (1994). Functional segregation of color and motion processing in the human visual cortex: clinical evidence. *Cerebral Cortex (New York, N.Y. : 1991)*, *4*(5), 555–72. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/7833656

Valdes-Sosa, M. Cobo, A. & Pinilla, T. (n.d.). Attention to object files defined by transparent motion.

Valdes-Sosa, M. Cobo, A. & Pinilla, T. (1998). Transparent motion and object-based attention. *Cognition*, *66*(2), B13–B23. doi:10.1016/S0010-0277(98)00012-2

Van Dam, W. O. & Hommel, B. (2010). How object-specific are object files? Evidence for integration by location. *Journal of Experimental Psychology: Human Perception and Performance*, *36*(5), 1184–1192.

Van Essen, D. C. & Zeki, S. M. (1978). The topographic organization of rhesus monkey prestriate cortex. *J. Physiol. 277*(1), 193–226. Retrieved from http://jp.physoc.org/content/277/1/193.short

Vandenberghe, R. Duncan, J. Dupont, P. Ward, R. Poline, J.-B. Bormans, G. … Orban, G. A. (1997). Attention to One or Two Features in Left or Right Visual Field: A Positron Emission Tomography Study. *J. Neurosci. 17*(10), 3739–3750. Retrieved from http://www.jneurosci.org/content/17/10/3739.short

Vanderhasselt, M.-A. De Raedt, R. Brunoni, A. R. Campanhã, C. Baeken, C. Remue, J. & Boggio, P. S. (2013). tDCS over the left prefrontal cortex enhances cognitive control for positive affective stimuli. *PloS One*, *8*(5), e62219. doi:10.1371/journal.pone.0062219

Varnava, A. Stokes, M. G. & Chambers, C. D. (2011). Reliability of the “observation of movement” method for determining motor threshold using transcranial magnetic stimulation. *Journal of Neuroscience Methods*, *201*(2), 327–332. Retrieved from http://www.sciencedirect.com/science/article/pii/S0165027011004754

Vogt, S. Taylor, P. & Hopkins, B. (2003). Visuomotor priming by pictures of hand postures: perspective matters. *Neuropsychologia*, *41*(8), 941–51. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/12667530

Von der Malsburg, C. (1981, May 9). The Correlation Theory of Brain Function. Retrieved from http://cogprints.org/1380/5/vdM_correlation.ps

Vuilleumier, P. (2000). Faces call for attention: evidence from patients with visual extinction. *Neuropsychologia*, *38*(5), 693–700. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/10689045

Wang, P. He, S. Fan, S. L. Liu, Z. X. & Chen, L. (2006). Perceptual asynchrony: motion leads color. *NeuroReport*, *17*(11), 1159–1163. Retrieved from http://www.ncbi.nlm.nih.gov/entrez/query.fcgi?cmd=Retrieve&db=PubMed&dopt=Citation&list_uids=16837846

Wei, P. Müller, H. J. Pollmann, S. & Zhou, X. (2011). Neural correlates of binding features within- or cross-dimensions in visual conjunction search: an fMRI study. *NeuroImage*, *57*(1), 235–41. doi:10.1016/j.neuroimage.2011.04.024

Weldon, M. S. (1993). The time course of perceptual and conceptual contributions to word fragment completion priming. *Journal of Experimental Psychology. Learning, Memory, and Cognition*, *19*(5), 1010–23. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/8409846

Weldon, M. S. & Jackson-Barrett, J. L. (1993). Why do pictures produce priming on the word-fragment completion test? A study of encoding and retrieval factors. *Memory & Cognition*, *21*(4), 519–28. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/8350743

Wheeler, M. E. & Treisman, A. M. (2002). Binding in short-term visual memory. *Journal of Experimental Psychology. General*, *131*(1), 48–64. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/11900102

Wojciulik, E. & Kanwisher, N. (1999). The Generality of Parietal Involvement in Visual Attention. *Neuron*, *23*(4), 747–764. Retrieved from http://www.sciencedirect.com/science/article/pii/S0896627301800337

Wojciulik, E. Kanwisher, N. & Driver, J. (1998). Covert Visual Attention Modulates Face-Specific Activity in the Human Fusiform Gyrus: fMRI Study. *J Neurophysiol*, *79*(3), 1574–1578. Retrieved from http://jn.physiology.org/content/79/3/1574.short

Woldorff, M. G. Hazlett, C. J. Fichtenholtz, H. M. Weissman, D. H. Dale, A. M. & Song, A. W. (n.d.). Functional parcellation of attentional control regions of the brain. *Journal of Cognitive Neuroscience*, *16*(1), 149–65. doi:10.1162/089892904322755638

Wolfe, J. M. (1998). *Visual search. Attention. Attention* (pp. 13–73).

Wolfe, J. M. & Bennett, S. C. (1997). Preattentive Object Files: Shapeless Bundles of Basic Features. *Vision Research*, *37*(1), 25–43. doi:10.1016/S0042-6989(96)00111-3

Wolfe, J. M. & Cave, K. R. (1999). The Psychophysical Evidence for a Binding Problem in Human Vision. *Neuron*, *24*(1), 11–17.

Wolfe, J. M. Cave, K. R. & Franzel, S. L. (1989). Guided search: An alternative to the feature integration model for visual search. *Journal of Experimental Psychology: Human Perception and Performance*, *15*(3), 419–433.

Woo, S.-H. Kim, K.-H. & Lee, K.-M. (2009). The role of the right posterior parietal cortex in temporal order judgment. *Brain and Cognition*, *69*(2), 337–43. doi:10.1016/j.bandc.2008.08.006

Wu, D.-A. Kanai, R. & Shimojo, S. (2004). Steady-state misbinding of color and motion. *Nature*, *429*(6989), 262.

Xu, J. (2010, December 10). Topological Structure and Analysis of Interconnection Networks. Springer Publishing Company, Incorporated. Retrieved from http://dl.acm.org/citation.cfm?id=1965102

Xu, Y. & Chun, M. M. (2006). Dissociable neural mechanisms supporting visual short-term memory for objects. *Nature*, *440*(7080), 91–5. doi:10.1038/nature04262

Yantis, S. (1998). Control of Visual Attention. *Attention*, *1*(1890), 223–256. doi:10.1093/acprof

Yantis, S. & Serences, J. T. (2003). Cortical mechanisms of space-based and object-based attentional control. *Current Opinion in Neurobiology*, *13*(2), 187–193. doi:10.1016/S0959-4388(03)00033-3

Yarkoni, T. Barch, D. M. Gray, J. R. Conturo, T. E. & Braver, T. S. (2009). BOLD correlates of trial-by-trial reaction time variability in gray and white matter: a multi-study fMRI analysis. *PloS One*, *4*(1), e4257. doi:10.1371/journal.pone.0004257

Yau, J. M. Pasupathy, A. Brincat, S. L. & Connor, C. E. (2013). Curvature processing dynamics in macaque area V4. *Cerebral Cortex (New York, N.Y. : 1991)*, *23*(1), 198–209. doi:10.1093/cercor/bhs004

Yeshurun, Y. Kimchi, R. Sha'shoua, G. & Carmel, T. (2009). Perceptual objects capture attention. *Vision Research*, *49*(10), 1329–35. doi:10.1016/j.visres.2008.01.014

Yi, D.-J. Turk-Browne, N. B. Flombaum, J. I. Kim, M.-S. Scholl, B. J. & Chun, M. M. (2008a). Spatiotemporal object continuity in human ventral visual cortex. *Proceedings of the National Academy of Sciences of the United States of America*, *105*(26), 8840–5. doi:10.1073/pnas.0802525105

Yi, D.-J. Turk-Browne, N. B. Flombaum, J. I. Kim, M.-S. Scholl, B. J. & Chun, M. M. (2008b). Spatiotemporal object continuity in human ventral visual cortex. *Proceedings of the National Academy of Sciences of the United States of America*, *105*(26), 8840–5. doi:10.1073/pnas.0802525105

Zeki, S. (1983). Colour coding in the cerebral cortex: The reaction of cells in monkey visual cortex to wavelengths and colours. *Neuroscience*, *9*(4), 741–765. Retrieved from http://www.sciencedirect.com/science/article/pii/0306452283902658

Zeki, S. (1991). Cerebral akinetopsia (visual motion blindness). A review. *Brain : A Journal of Neurology*, *114 (Pt 2*, 811–24. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/2043951

Zeki, S. Kennard, C. Watson, J. D. G. Lueck, C. J. & Frackowiak, R. S. J. (1991). Cortex of Functional Specialization in Human Visual, *17*(March).

Zeki, S. M. (1973). Colour coding in rhesus monkey prestriate cortex. *Brain Research. Cognitive Brain Research*, *53*, 422–427.

Zeki, S. M. (1976). The projections to the superior temporal sulcus from areas 17 and 18 in the rhesus monkey. *Proceedings of the Royal Society B: Biological Sciences*, *193*, 199–207.

Zeki, S. Watson, J. Lueck, C. Friston, K. Kennard, C. & Frackowiak, R. (1991). A direct demonstration of functional specialization in human visual cortex. *J. Neurosci. 11*(3), 641–649. Retrieved from http://www.jneurosci.org/content/11/3/641.short

Zmigrod, S. & Hommel, B. (2009). Auditory event files: integrating auditory perception and action planning. *Attention, Perception & Psychophysics*, *71*(2), 352–362.

Appendices - Appendix A

Experiment 2C

Introduction

Hommel (2002) has shown that, when forming an object representation, the integration of features also entails information concerning the action that the object affords. In order to distinguish and quantify the contribution of motor response priming from that of perceptual priming, the reviewing paradigm was further modified. The modification involved changing S1 to a stimulus that would represent only the motor response and not overlap perceptually with the stimulus presented in S2. S2 would continue to be identical to the stimulus presented in experiment 2A and 2B: red or green dots moving either up or down. Participants were instructed to respond to the relative feature in S2 as fast as possible with either a left or right button press. Trials could either be congruent or incongruent with the motor action that was primed in S1. It was predicted that incongruent trials would lead to an increase in RT and an increase in error rates.

This final experiment looked to isolate the RT benefit and cost observed when a stimulus in S1 was not perceptually linked to S2, but instead acted purely as a motor response prime. S2 could either be motor congruent or motor incongruent with S1. Previous experiments have shown that observing finger movements strongly influences movement execution, irrespective of whether the finger movement was the relevant or the irrelevant stimulus dimension. This has been termed visuo-motor priming. However, although visuo-motor priming effects have been demonstrated robustly in numerous studies (Brass, Bekkering, Wohlschläger, & Prinz, 2000; Craighero, Fadiga, Umiltà, & Rizzolatti, 1996; Vogt, Taylor, & Hopkins, 2003), other studies, such as Cant, Westwood, Valyear & Goodale (2005), fail to find visuo-motor priming effects and therefore the factors causally influencing remains unclear.

If we successfully prime the motor action with the image of the finger associated with either the left/right button press, we should see a motor congruency effect. This should lead to faster responses than if the image presented is incongruent with the motor action required by the target.

A1.2 Method and Materials

A.2.1 Participants

The participants remained consistent throughout experiment 2A, 2B and 2C.

A1.2.3 Procedure and Design

The design was identical to experiment 2A with the following exceptions: S1 consisted of a picture of a right hand with either the index or the middle finger circled. Participants were also told to watch the preview screen but informed that it had no implications on the stimulus to follow during S2. The motor image presented during S1 was congruent for 50 % of the trials and incongruent for the remaining trials. The amount of trials and blocks were identical to experiment 2A and 2B. An example of the sequence of a trial is shown below in figure 3.5.

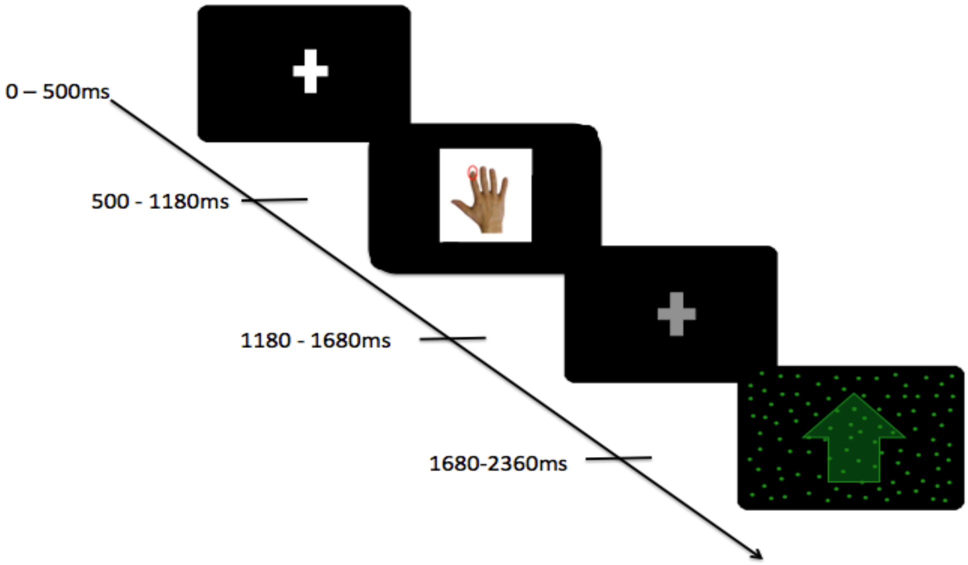
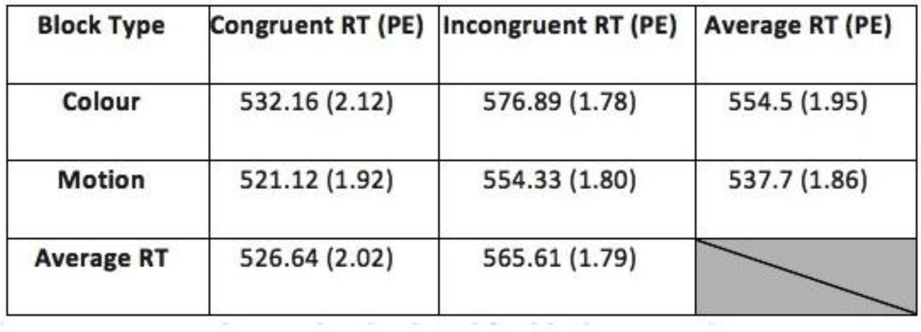


Figure A1.2.1. Schematic Illustration of the Displays and Timings of Events in Experiment 2C.

A1.3 Results

A 2x2 repeated measures ANOVA was carried out on both the RT data and PE data. Table A1.1 presents the average RT for the congruent and incongruent conditions as a function of block type (colour and motion) and collapsed across both block types.

Table A1.1 The Average RT in congruent\incongruent trials in either a colour or motion block. The average of both blocks are also presentd. The PE is presented in brackets.



Block Type	Congruent RT (PE)	Incongruent RT (PE)	Average RT (PE)
Colour	532.16 (2.12)	576.89 (1.78)	554.5 (1.95)
Motion	521.12 (1.92)	554.33 (1.80)	537.7 (1.86)
Average RT	526.64 (2.02)	565.61 (1.79)	

***Note*. The average RT and PE is also displayed for block type and congruency. RT = reaction time; PE = percentage error.**

A1.3.1 Congruency

The mean RT and PEs are presented in table A1.4. The ANOVA revealed a significant main effect of congruency between the RT in the congruent condition (M=526.64, SE=5.76) and the RT in the incongruent condition (M=565.61, SE=7.14), F(1,29)=35.5, P=0.00, partial η^2 =0.550. Further to this, the ANOVA revealed that there was a significant effect of block type with participants responding to colour slower (M=554.5 msecs, SE=8.035) than motion (M=537.7, SE=8.035), F (1,29)=5.224,P=0.03, partial η^2 =0.153. However, there was not a significant interaction between congruency and block type, F (1,29)=0.571, P=0.456, partial η^2 =0.019.

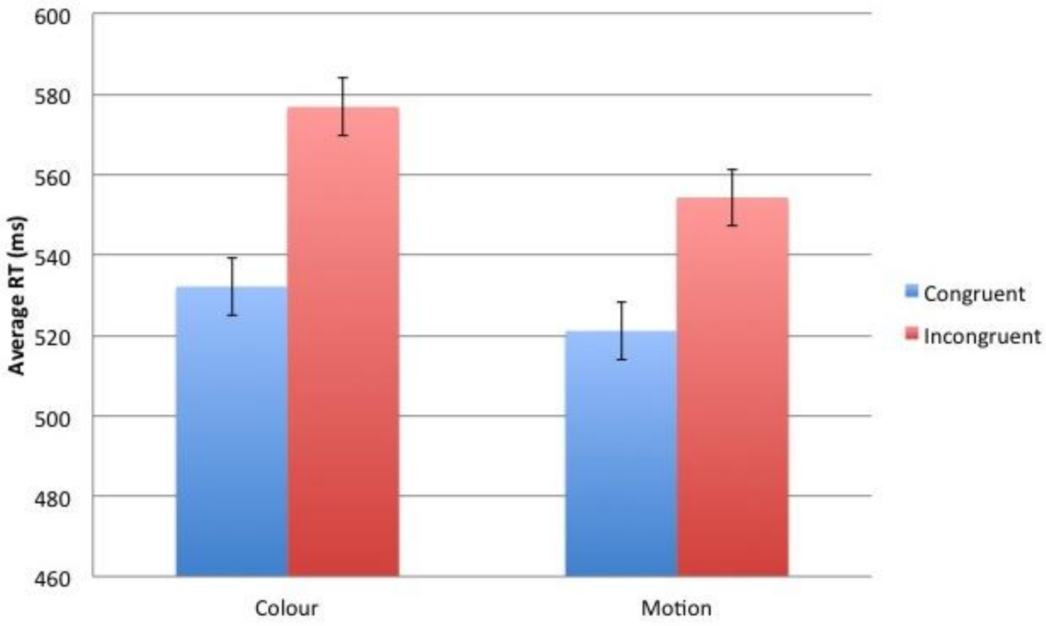


Figure A1.2. Graphical Representation of RT as a Function of Congruecy. Results demonstrate that participants responded faster to colour than motion and responded faster overall when the target stimuli was preceded by a picture of the congruent motor action. RT = reaction time. Error bars = SEM.

A1.3.2 Errors

A 2x2 ANOVA was carried out on the PEs across conditions and block type. The PE's are displayed within brackets in table 3.3. The ANOVA revealed that there was no significant difference between conditions, F (1,29)=0.22, P=0.883, partial η^2 =0.001. Further to this, there was no significant difference in the PEs between block type, F (1,29)=0.390 P=0.537, partial η^2 =0.013. The ANOVA further revealed that there was not a significant interaction between condition and block type (F (1,29)=0.131, P=0.720, partial η^2 =0.004.

A1.4 Discussion

Experiment 2C was successful in demonstrating that there is a response priming effect. By using an image of a motor response that shared no perceptual features with the target object, we were able to isolate and quantify the impact of a response priming effect. The average response congruency effect was 39ms. The results support previous data that shows that the observation of an object does not merely lead to categorization in order to comprehend it, but is sufficient to lead to the activation of the motor response afforded by that object.

This supports previous experiments that have shown that action observation can facilitate recognition of an object that typically involves a similar action. The action priming effect also supports the notion that action representations play a functional part in object recognition.

This confirms the necessity to avoid confounding stimulus repetition effects with response repetition effects.