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# **Do You Bind? The Representation of Visual Features and Objects in Working Memory**

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A thesis submitted in partial fulfilment of the requirements for the degree of  
Doctor of Philosophy in Psychology, The University of Auckland, January 2013

## Acknowledgments

Many thanks to my supervisors Mike Corballis and Tony Lambert for all their help, guidance and patience over the years. I am also indebted to other academic staff at the University of Auckland: Donna Rose Addis for her mentoring; Lynette Tippett for her insight in lab meetings; and lastly, Barry Hughes for providing me with a theoretical foundation in visual cognition.

This help was supplemented by many fellow graduate students. I especially thank Gjurgjica Badzakova-Trajkov for providing motivation towards the end. I thank Carolyn Wu and Victoria Martin for all their help, and apologise for relentlessly bugging Victoria on g-chat. Thanks to Lincoln Colling for our discussions about what constitutes an explanation in cognitive science. Many thanks to Georgina Parr for keeping me sane when working in “the dungeon”.

I thank all my family, both in New Zealand and South Africa, for all their support. This is especially true for my parents, Keith and Nonette, who have been an incredible inspiration to me, and to whom I am forever grateful.

Lastly, I dedicate this thesis to Sox, my beautiful wife. I could have never done this without you.

## Abstract

A central debate in visual working memory research centres on the nature of visual working memory representations. The object account proposes that the fundamental units of visual working memory are integrated representations, such that items are stored in working memory in an all-or-none fashion. The feature-channel account, on the other hand, proposes that visual features are stored independently of each other. According to this account, additional representations are required to code for the associations between visual feature dimensions.

Change-detection tasks are a commonly used paradigm to investigate the representational format of visual working memory. Performance in detecting novel visual features (novel changes) can be compared with detecting a recombination of visual features (binding changes) in this paradigm. While presenting a single-item as test display produces equal performance in novel and binding changes, there is disagreement about whether multi-item displays preferentially disrupt performance in binding changes. In *Study 1*, I showed that while a multi-item test display results in worse performance for binding conditions relative to novel colour and novel letter conditions when novel locations are used for the test display, this effect is alleviated if an informative retroactive cue is presented in the delay period.

In *Study 2*, I used a two-alternative forced choice task to investigate the representational format of visual working memory. Participants were presented with three coloured shapes which they had to maintain in visual working memory. They were then presented with two items and had to select, using the mouse, which item was from the original display (the target). The other item (the lure) was either a recombination of visual features from the original memory display (binding condition) or contained a novel visual feature (novel colour

and novel shape conditions). Mouse trajectories showed greater complexity and curvature for the binding condition, supporting the hypothesis that visual working memory stores information in parallel visual-feature channels.

*Study 3* explored whether the critical process disrupting working memory for binding information in change-detection tasks with multi-item test displays tasks is the perceptual binding of visual features. This was achieved by presenting two versions of a secondary visual search task in the delay period of a change-detection task with a single-item test display. One was a conjunction search which required the binding of visual features; the other was a “pop-out” search. Only the conjunction search task disrupted working memory for binding information more so than maintenance of visual features.

Finally, a neural-cognitive model is proposed that highlights the role of posterior parietal regions in coordinating the binding of visual features across the domains of visual perception and visual working memory.

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## **Chapter 1: General Introduction**

### **1.1 Introduction**

This thesis concerns a central topic in visual cognition: the nature of short-lived, visual memory traces that linger in the mind after a stimulus has disappeared from one's field of view. Due to the frequency of head and eye movements in daily life, and the constantly changing environments we inhabit, these memory traces play a vital role in the cascade of information processing that occurs between sensation and behaviour. That is, our behaviour at any given moment is contingent not only on our current visual experience, but on visual experiences just past. The cognitive faculty to which these memory traces are generally attributed is working memory, defined as the maintenance and manipulation of information over short periods of time (Baddeley & Hitch, 1974; Baddeley, 1983, 1986, 2002).

Given its importance in driving intelligent behaviour, it is no surprise that the short-term retention of information has been the subject of an extensive body of research in the cognitive psychology literature, beginning with George Miller's review of capacity limits in verbal short-term memory (Miller, 1956), which proposed that the number of items able to be maintained over short periods of time is roughly seven items (give or take a couple). Importantly, this upper limit is largely independent of the informational complexity of the items themselves. Thus, similar capacity limits are found for binary digits, decimal digits, letters, digits and monosyllabic words. Motivated largely by developments in communications and information theory, Broadbent (1958) went on to develop a model of short-term storage of information (immediate memory in his terminology) based on the finding that the reporting of a series of digits, presented to both ears simultaneously, is not done so in the sequence they were presented. Instead, all the letters presented to one ear are reported first, followed by the letters presented to the other ear. This suggested that

information presented to one ear (or channel) is temporarily held in a buffer while the information from the other ear is being processed for verbal report. In a similar vein, Sperling (1960) posited an iconic memory: the initial sensory buffer of visual information. He showed in experiment 1 that, when participants were presented with displays of 3 to 12 letters (configured in a variety of ways, from single lines of letters to equally spaced rows), they were able to correctly recall an average of 4.3 letters. This “immediate memory span” was largely independent of the set size of the original display i.e. performance was similar from set sizes 4 to 12. In experiment 3, Sperling went on to assess performance when participants were cued, by tones of varying pitch, to report only a single row of letters out a display. In this version of the task, set sizes ranged from 6 (2 rows of 3 letters) to 12 (3 rows of 4 letters). The key finding was that participants were generally able to recall all of the letters on the cued row, suggesting that all of the letters in the display are initially available for report but are quickly lost in the full report version of the task (experiment 1). The relationship of iconic memory to other forms of information retention will be discussed further below, but the findings of Sperling (1960) support an initial high-capacity buffer of visual information.

These initial forays into the study of short-term retention of information contributed to the development of the modal model of human memory (the foremost of which was developed by Atkinson & Shiffrin, 1968), which drew sharp distinctions between three separate memory stores: a sensory register, a short-term store and a long-term store. According to such models, information is selected from the sensory stores through a serial scanning process, while a concurrent searching process occurs in long-term memory matching sensory information to semantic knowledge. It is these semantic (or verbal) representations that are then transferred from the long-term to the short-term store (Atkinson & Shiffrin, 1968). Transfer in the opposite direction, from the short-term to long-term store, occurs if information held in the short-term store is rehearsed by an individual and is lost to decay if no rehearsal occurs. This

relationship between short and long-term memory is, according to modal models, the basis of the well-known primacy and recency effects observed in list-learning paradigms: items presented earlier in the list are more likely to be rehearsed and transferred to long-term memory (primacy effect), while the items presented last show increased levels of recall due to them still being available in short-term memory. Importantly, the short-term store of Atkinson and Shiffrin (1968, 1971) had the dual properties of being a temporary storage buffer as well as the locus of the contents of awareness: "... we tend to equate the short-term store with "consciousness"... the thoughts and information of which we are currently aware" (1971, p. 83).

Baddeley (1976, 1997), offers a number of criticisms of this model, two of which are mentioned here. The first is the claim that the short-term store of Atkinson and Shiffrin (1968) is a unitary system, unlike the sensory stores that feed into it that are specific to particular modalities (echoic memory, iconic memory etc.). As will be discussed in more detail below, however, a mass of experimental research has shown there to be robust modality effects on the short-term maintenance of information, making a unitary short-term store highly unlikely. Second, a number of neuropsychological cases have shed doubt on storage in long-term memory being contingent on a short-term store. Shallice and Warrington (1970) presented results from patient KF, who suffered a left parietal injury, that show a strikingly low short-term memory capacity (as measured by digit span) coupled with a largely intact long-term memory (as measured by paired associate learning and word learning paradigms). The importance of left temporoparietal regions for short-term memory (but not long-term memory encoding) was further illustrated in subsequent studies showing that damage to these areas results in normal performance in long-term memory tasks in conjunction with considerable short-term memory deficits (Risse, Rubens, & Jordan, 1984; Warrington, Logue, & Pratt, 1971). An interesting feature of such patients is that while they

showed signs of a remarkably reduced short-term store capacity, many of them led conspicuously normal lives, performing their vocational duties as taxi drivers, secretaries and shop keepers successfully (Baddeley, 2007). This calls into the question the notion, proposed by Atkinson and Shiffrin, that the short-term store described by modal models (a unitary buffer) is a necessary requirement for general cognition.

## **1.2. The Baddeley model of working memory**

Seeking to clarify the role short-term memory plays in general cognition and information processing (learning, problem-solving, reasoning, comprehension etc.), Baddeley and Hitch (1974) developed a model of working memory (the Baddeley model hereafter), which, after more than three decades (and some revisions), is still the dominant model in the relevant literature. Whereas modal models of memory tended to view short-term memory as solely a storage buffer, where information is either lost or transferred to long-term stores, the Baddeley model of working memory is one of a “*control system* with limits on both its storage and processing” (Baddeley and Hitch, 1974, p86, my italics), performing an intrinsic role in driving intelligent behaviour and much of what we generally regard as *thinking*. As recounted by Baddeley (1976), his work characterising the working memory system was motivated by determining the functional value of a short-term memory in general cognition “beyond that of keeping experimental psychologists busy” (p. 169).

To this end, Baddeley and Hitch (1974) employed a now widespread paradigm in cognitive psychology — the dual task — to determine the effect of maintaining information in short-term memory on verbal reasoning, language comprehension and long-term memory. The authors reasoned that if these faculties were reliant on a short-term memory store whose sole function was the temporary storage of information, then increasing the number of items held in that store should result disruptions in performance across the three tasks. Two

important findings emerged from their series of experiments: the first was that loading the short-term store with a small number of items (2-3 digits) had very small, non-significant effects (or no effect at all) on the three tasks; secondly, increasing the load to close to short-term memory capacity (6 digits) resulted in significant decreases in performance across all tasks, although participants were still able to perform well in reasoning, comprehension and long-term learning tasks.

The short-term store envisaged by modal models — one characterised solely as a storage buffer — is unable to account for these findings. If such a short-term storage buffer was necessary for the cognitive processes investigated by Baddeley and Hitch (1974), performance should have been near floor when participants were simultaneously maintaining 6 items in short-term memory. In addition, there should have been some disruption in the cognitive tasks when maintaining 2-3 items. However, the results do not suggest that cognition (as indexed by the three tasks investigated by Baddeley and Hitch) is entirely independent of a short-term memory buffer, as shown by the moderate dual-task effects when the memory set size was 6 items.

To account for the findings from their series of dual-task experiments, Baddeley and Hitch (1974) proposed a working memory system that extends beyond the simple storage of information for short periods. The proposed limited-capacity workspace included components specialised for storage as well as the general processing of information. Namely, Baddeley and Hitch (1974) proposed a “slave system” dedicated to the storage of information and a central executive sensitive to “control processing demands” (p. 76) but also capable of information storage when the capacity of the storage buffer was exceeded. Initially, the slave system was restricted to verbal information (the phonological loop), but later a buffer responsible for maintaining visuo-spatial information (the visuo-spatial sketchpad) was added to the model (Baddeley, 1986). Later still, Baddeley (2000) introduced a fourth component to

the model: the episodic buffer. In the following sections, I characterise and, where appropriate, critique these components of the Baddeley model.

### **1.2.1 The slave systems**

There is a large body of evidence — from neuropsychological, neuroimaging and behavioural studies — that strongly supports the notion that working memory storage is fractionated i.e. that the storage of visual and verbal information are largely independent processes.

Owen, Morris, Sahakian, Polkey, & Robbins (1996) have shown differences in the behavioural profiles of three patient populations (frontal lobe damage, temporal lobe excisions and amygdalo-hippocampectomy patients) in tests of verbal, spatial and visual working memory. While the frontal lobe population showed substantial deficits in a spatial memory task (the search for tokens hidden in boxes<sup>1</sup>), this deficit was only present in the other two patient groups at large set sizes. Importantly, this difference between the groups did not extend to an analogous verbal memory task in which participants searched for tokens on a monitor that were hidden behind common surnames. The location of these names changed from trial to trial, so spatial information was entirely non-informative and performance was measured by how often participants search for a token behind already inspected surnames. In addition, the amygdalo-hippocampectomy and temporal lobe patients showed deficits in a version of the task requiring memory for objects (as in the surname version of the task, locations changed from trial to trial), while the frontal lobe patients behaved similarly to controls. This last finding suggests a further fractionation of working memory is required for visual and spatial information — an issue that will be discussed in greater detail below. It is

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<sup>1</sup> In these tasks, performance is measured by counting how often participants return to locations already searched.

important to note, however, that this study failed to produce a true double dissociation as all patient groups exhibited normal performance in the verbal working memory task.

Taken together, the results of Vallar and Baddeley (1984) and Hanley, Young, and Pearson (1991) do, however, provide such a dissociation. Vallar and Baddeley (1984) showed that patient PV, who had an ischemic lesion to “language areas” of the left hemisphere, showed performance deficits for verbal working memory (but not verbal long-term memory), while presenting with normal visuospatial working memory performance. On the other hand, Hanley et al. (1991) reported findings from patient ELD — who suffered damage to the frontal aspect of the right Sylvian fissure — who showed normal verbal working memory for letters (regardless of modality of presentation), while also showing substantial deficits in performance in tasks requiring spatial working memory (Corsi Blocks and the Brooks Matrix).

In addition to the neuropsychological evidence, double dissociations between verbal and visuospatial working memory have long been reported in behavioural studies using normal controls. These typically take the form of a dual-task procedure, in which secondary tasks requiring either visuospatial or verbal processes differentially impact performance on visuospatial and verbal short-term memory tasks. For example, Logie, Zucco, and Baddeley (1990) have shown that performance in visuospatial and verbal short-term tasks are affected to differing degrees by arithmetic and visual imagery tasks: performance in a letter span task is more affected by the arithmetic task than the imagery task, while the opposite effect is true for the visual span task. As noted by Smith and Jonides (1993) however, such dual-task designs should be treated with caution for two reasons. First, the secondary tasks are often very complex and may require additional cognitive processes beyond those of interest. For example, while the arithmetic task employed by Logie et al. (1990) no doubt involves a verbal component, it has become increasingly clear that such simple arithmetic is tightly

linked to spatial processing and spatial attention, as shown by behavioural tasks (e.g. Fischer, Castel, Dodd, & Pratt, 2003) and neuroimaging work (Dehaene, Piazza, Pinel, & Cohen, 2003; Knops, Thirion, Hubbard, Michel, & Dehaene, 2009). Second, many visual secondary tasks used in such dual-task designs involve mental imagery (and not visual processing *per se*). And, as Pylyshyn (1981, 2003) has long argued, there need not be anything *visual* associated with mental imagery; instead, imagery could involve tacit, propositional knowledge *about* visual processes.

Cocchini, Logie, Della Sala, MacPherson and Baddeley (2002) have used a more direct dual-task methodology to assess the independence of visuospatial and verbal working memory. In their study, participants performed visual and verbal memory tasks under a range of conditions. First, visual and verbal memory tasks were performed in isolation. Next, each task was paired with either a visuospatial or verbal secondary task, or, in the critical conditions, with the *other* memory task. That is, in these dual-memory conditions, each memory task played the role of a secondary task to the other memory task. The results showed that while the visuospatial secondary task affected visual memory (and not verbal memory), the verbal memory task did not. Likewise, the visual memory task only minimally disrupted performance in the verbal memory task. The negligible impact of maintaining one form of information on the successful maintenance of the other is strongly suggestive of a working memory system composing separate buffers for verbal and visuospatial information.

The clear demarcation of verbal and visuospatial working memory is less clear when surveying the neuroimaging literature, however. Rämä, Sala, Gillen, Pekar, and Courtney (2001) have provided evidence that the maintenance of verbal and visual information in working memory recruits different neural circuits under certain conditions. In their fMRI study, participants were required to perform match-to-sample tasks for famous and non-famous faces and names. BOLD signal differences were found between faces and names in a

number of regions. The results suggest that lateralisation of information type (names versus faces) is a major organising principle in working memory maintenance, with right hemisphere regions (fusiform gyrus and a number of frontal regions – inferior frontal, precentral, and superior medial frontal gyri) being specialised for visual information and left hemisphere regions (insula, precuneus, inferior frontal and pre and post-central gyri) for verbal information. Interestingly, this finding was only apparent when the names and faces were non-famous, suggesting that famous faces and names resulted in the maintenance of both verbal and visual representations in working memory (as evidenced by the co-activation of visual and verbal areas for both faces and names). The principle of lateralisation is also evident when contrasting verbal and spatial working memory. Reuter-Lorenz and colleagues (2000) used positron emission tomography (PET) to compare delay period activity during a verbal and spatial working memory task, and showed laterality effects (verbal > spatial in left hemisphere; spatial > verbal in right hemisphere) in dorsolateral and ventral prefrontal cortices, supplementary motor areas, and inferior frontal gyri (Broca's area).

Given the importance of replication in neuroimaging studies (Poldrack et al., 2008), it is telling that these findings are not universally agreed upon. Importantly, a meta-analysis of 60 PET and fMRI studies has shown no evidence for a distinction between verbal, visual and spatial information storage in the prefrontal cortex (Wager & Smith, 2003). Instead, prefrontal regions tended to be sensitive to the extent of executive demand, as well as to the specific type of executive process.

While the specificity of prefrontal regions to different information types is questionable, there is some evidence that visuospatial and verbal working memory recruit different sensory, perceptual and/or language regions of the brain. For example, verbal working memory tasks consistently activate Broca's area (Chein & Fiez, 2001; Chein, Fissell, Jacobs, & Fiez, 2002; Fiez et al., 1996; Gruber & von Cramon, 2003; Paulesu, Frith, & Frackowiak, 1993; Schulze,

Zysset, Mueller, Friederici, & Koelsch, 2011). This is interesting for two reasons: first, it is likely that this activation is the locus of sub-vocal rehearsal processes proposed to operate on the contents of verbal working memory, enabling this information to be maintained in working memory (Baddeley, 2003); second, the activation of Broca's area by verbal memory tasks and language comprehension tasks (e.g. Santi & Grodzinsky, 2010, 2012; Wang et al., 2008) illustrates nicely the intimate relationship between language and working memory processes. Indeed, some authors have suggested that the emergence of working memory in homo sapiens' cognitive toolkit was a major development in language and creativity in our evolutionary past (Coolidge & Wynn, 2005).

While verbal working memory activates, amongst others, regions also involved in language perception, visuospatial working memory recruits posterior regions of the brain involved in the initial sensory and perceptual processing of visuospatial information. For example, the maintenance of pictures of houses in working memory maps onto sustained BOLD signal in parahippocampal place area, while signal in the fusiform face area remains elevated during the maintenance of faces (Ranganath, Cohen, Dam, & D'Esposito, 2004). Harrison and Tong (2009) have used a fairly novel fMRI analysis technique called multivoxel pattern analysis (MVPA) to show that decoding signals in early visual areas (V1-V4) is able to reliably determine the orientation of a sine grating maintained in visual working memory.

Taken together, an overwhelmingly strong case can be made on the basis of the extant behavioural, neuropsychological and neuroimaging evidence that working memory does not rely on a singular storage buffer, but is instead best modelled by a system containing two separate subsystems — one for verbal, the other for visuospatial information. One issue that requires closer examination is the degree of independence between the two slave systems. While Baddeley and his collaborators posit a sharp distinction between visual and verbal domains in working memory (Cocchini et al, 2002), there is evidence supporting cross-

domain limits. Morey and Cowan (2004) make the point that Cocchini et al. failed to separate performance on the main memory task based on performance in the secondary memory task. In addition, it could be that the reason a dual-task effect was not found for the simultaneous maintenance of visual and verbal information was that the information loads were sub-capacity for both domains. To address these concerns, Morey and Cowan (2004) used a visual working memory paradigm requiring the maintenance of 4, 6 or 8 items in working memory; the latter two set sizes exceed the capacity of visual working memory of 3-4 items (Luck & Vogel, 1997). In addition, the secondary task was an articulatory task that required the repeated vocalisations of either the participant's phone number, a 2-digit number (low verbal memory load) or a 7-digit number (high verbal memory load). Finally, the authors assessed visual working memory performance not only according to the articulatory condition, but also according to accuracy in the high verbal memory load condition i.e. post-hoc "*7-Digits-Correct*" and "*7-Digits-Error*" conditions were created. The results showed that while a 2-digit load had no effect on visual working memory performance, maintaining 7 digits in working memory resulted in severe decrements in performance in the visual memory task at all set sizes. Importantly, this decrement was greater when the visual task was paired with *7-Digits-Error* condition compared to the *7-Digits-Correct* condition. According to the authors, this suggests a common workspace for visual and verbal information in working memory.

This interpretation seems overly strong, however. An alternative explanation is that while there are separate storage buffers for visual and verbal working memory, they both rely on a single, central executive resource. Indeed, this is exactly what the Baddeley model entails. Under this theoretical framework, the pattern of results reported by Morey and Cowan (2004) is due to insufficient executive resources available to both visual and verbal buffers, thereby resulting in reduced performance.

A second issue with the dual-storage model of working memory is that it is silent on the short-term maintenance of information types that are neither visual nor verbal in nature. It is now firmly established that transient memory traces exist for a vast array of sensory, perceptual and motor domains. For example, a distinct olfactory working memory has been reported by Dade, Zatorre, Evans, and Jones-Gotman (2001). Fiore et al. (2012) have reported findings suggesting a short-term memory for flavours. Likewise, the short-term maintenance of tactile information has been shown to recruit distinct neural regions (e.g. somatosensory cortex) from verbal and visuospatial working memory (Harris, Harris, & Diamond, 2001; Harris, Miniussi, Harris, & Diamond, 2002). Working memory has been shown for tonal information (Schulze et al., 2011). Interestingly, this is distinct from the maintenance of loudness information (Clément, Demany, & Semal, 1999). Lastly, there exists a specialised buffer for the transient maintenance of movement configurations (Smyth & Pendleton, 1989), which is independent of spatial working memory (Cortese & Rossi-Arnaud, 2010).

A possible reason for the absence of these buffers in the Baddeley model may be entirely pragmatic: visual and verbal information most likely composes a large majority of the information we encounter in our daily lives, and therefore maintain in our working memory. In addition, these sorts of information are most amenable to scientific investigation, as they can be easily and rigorously studied using computers to present stimuli with precision — something not possible with, for example, gustatory or olfactory stimuli. The fact that these buffers do exist, however, suggests that a fuller, more complete version of the Baddeley model is required<sup>2</sup>.

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<sup>2</sup> Such a model would, however, lack the parsimony for which the Baddeley model is well known. Instead it would become “an increasingly complex taxonomy of boxes and arrows linking each independent storage buffer (or subbuffer) to the Central Executive” (Postle, 2006, p. 25).

### **1.2.2. The central executive**

While the partitioning of short-term storage into verbal and visuospatial domains was important, it was, if viewed in isolation, more a refinement of previous short-term memory models than a significant conceptual advance. It was the addition of a central executive to Baddeley's model and the explicit linking of the working memory system to the control of intelligent behaviour (Baddeley & Hitch, 1974) that provided the most noteworthy break from previous models. It is striking then, that the central executive has proven to be the most difficult component to characterise, as well as the component on which the least experimentation has focussed. Indeed, Baddeley has conceded that it "represents the most complex aspect of working memory and the most difficult to both analyse and conceptualise" (Baddeley, 1983, p. 315).

Initially, the central executive was endowed with the dual functions of short-term storage and an underspecified capability for general-purpose processing (Baddeley & Hitch, 1974), although the storage aspect of the central executive was later removed (Baddeley, 1986). Baddeley (1986), in an attempt to pin down the functional details of this important component of working memory, drew heavily on the Supervisory Attentional System (SAS) proposed by Norman and Shallice (1980), which drew a distinction between behaviours that are automatic compared to those that require attention and are under wilful control. While the precise details of the SAS model are beyond the scope of — and tangential to — the current thesis, it should suffice to describe the basic properties of these two types of behaviour. Automatic behaviours arise from a linear sequence consisting of perceptual representations activating specific schemas above a threshold, which then trigger specific motor outputs.

Controlled behaviours, on the other hand, involve conflict or competition between schemas and fall into at least one of the following five categories — behaviours that: involve planning/decision making; require “troubleshooting”; are relatively novel; are regarded as difficult or dangerous; involve suppressing an otherwise habitual response. Schema conflict is resolved by the SAS, which does so by representing the past and present states of the environment and one’s goals and intentions. In a similar vein, the central executive, according to Baddeley (e.g. Baddeley & Logie, 1999), coordinates the short-term retention of information so as to maximise performance in cognitive tasks e.g. language comprehension, problem solving, arithmetic etc.

As Parkin (1998) has noted, however, the functional properties of Baddeley’s central executive are so ill-defined, yet so explanatorily powerful, that it merely plays the role of a homunculus in psychological explanation. That is, by describing the properties of the central executive in personal, intentional terms (e.g. controlling, supervising, coordinating), the central executive simply becomes a “little man” in our heads who does the hard cognitive work for us. To borrow (and modify) a phrase from Fodor (1999): *This* is the way we do dual-tasks: we notify a little man in our heads who does it for us. Baddeley, in a number of writings (Baddeley & Logie, 1999; Baddeley, 1996, 1998b), has explicitly agreed that, in its current guise, the central executive does indeed have many of the properties of a homunculus, but that this does not necessarily render the construct impotent in psychological explanation. Instead, the central executive currently plays the role of a temporary stop-gap until further research is carried out that can decompose it into its constituent parts (some candidate subcomponent processes are discussed below). This is similar to the strategy of Dennett (1981), who defends the use of intentional terms in explaining behaviour as long as we eventually “cash them out” for sub-personal, non-intentional descriptions once an appropriate mechanism has been specified. This breaking down of homunculi occurs by

specifying increasingly *less* intelligent components at each stage of decomposition (Dennett, 1981, 1991).

Such a strategy is exemplified by Baddeley (1996), who outlines four potential central executive subcomponents responsible for: the coordination of the slave systems in dual-task procedures; the switching of retrieval strategies in random number generation tasks; selectively attending to certain classes or dimensions of stimuli while inhibiting others; the activation of long-term memory representations. This treatment was, given the lack of experimental data at the time, necessarily tentative and speculative. More recent attempts at fractionating the homuncular executive have been more precise. Hazy, Frank, and O'Reilly (2006, 2007) have developed a sophisticated neurocomputational model — the prefrontal cortex/ basal ganglia (PBWM) model — that replicates human performance in a number of working memory tasks relying heavily on executive function. Importantly, they fractionate executive function both anatomically and computationally.

Anatomically, they distribute working memory function across three processing modules: posterior cortex (sensory and motor processing, encoding of information), the hippocampus (binding of information, rapid learning) and prefrontal cortex/basal ganglia (PFC: maintenance of important goal-directed and contextual information; BG: dynamic updating of this information). Functionally, they propose six components of the central executive, and use the 1-2-AX task as a concrete example to illustrate these components. In this task, participants are presented with a sequence of letters and digits and are required to press the right key upon presentation of a target sequence, and the left key for all other stimuli. The current target sequence is denoted by the last seen cue. For example, presentation of a 1 specifies a target sequence of an A followed by an X, while presentation of a 2 specifies a target sequence of a B followed by a Y. In this example, the following sequence 1-A-X-B-X-2-B-Y would require the following response sequence L-L-R-L-L-L-L-R. In addition,

distractor stimuli (e.g. 3,F) are interspersed throughout the sequence and are to be ignored i.e. they not responded to, and do not play a role in decoding stimuli sequences (A-F-X is functionally equivalent to A-X) . This complicated task draws heavily on executive function, and Hayes and colleagues propose this is grounded in the interaction of six subcomponents: *rapid updating* (the rapid encoding and maintenance of new information into working memory); *robust maintenance* in spite of continual processing of subsequent stimuli; *distinct working memory representations* (e.g. maintaining cue information separate from target information); *selective updating* of some information (e.g. discarding previous stimulus if it is task irrelevant) while maintaining relevant task demands (e.g. last cue was a 1); *top-down biasing* of processing of information e.g. stimulus-response contingencies depend on the currently maintained cue; *learning the gating demands of the task*, such that gating is closed for distractors (i.e. filtered) and opened for task relevant stimuli.

In addition, the behaviour of the components of the PBWM model do not rely on any built-in knowledge imposed on the system by the designers. For example, the correct filtering of distractors is not hard-coded into the model (e.g. “if stimulus = F, then ignore”), but is instead learned entirely by trial and error. This is important because, as Hazy et al. (2006) note, building knowledge directly into a component would mean that it too would be an homunculus of sorts.

I describe the model of Hazy et al. (2006) here in a fair amount of detail, not because it is necessarily “true”, but because it illustrates nicely what homuncular decomposition should look like. If cognitive science is to produce explanatory models of human cognition, invoking an amorphous central executive will have to, at some stage, give way to models that describe behaviour as the interaction of much simpler processes.

### **1.2.3. The episodic buffer**

Confronted by a range of findings not easily explained by his three component model of working memory, Baddeley (2000) modified his model to include a fourth component he called the episodic buffer. This new component is hypothesised to be intimately linked to the central executive and is responsible for representing entire episodes via the maintenance of multimodal information. In addition, the episodic buffer mediates the relationship between working and long-term memory (Baddeley, 2000, 2002, 2012). The relationship with long-term memory is especially important for facilitating chunking in working memory when comprehending complex prose. As the number of words in such passages far exceed the capacity of the phonological loop, Baddeley (2000) proposes that the episodic buffer makes use of knowledge regarding the structure of language and conceptual schemas in long-term memory to aid storage in working memory.

It is the process of binding, however, which has received the most attention in active research on the episodic buffer. The issue of integrating information between the slave systems was highlighted by work showing that visual information modulates performance on a verbal recall task (Logie, Della Sala, Wynn, & Baddeley, 2000). Specifically, it was reported that visual similarity, either at the level of words (e.g. *fly*, *ply*, *cry* vs. *tie*, *guy*, *rye*) or letters (*K/k* vs. *Q/q*), reduced performance in serial recall for verbal information, suggesting that visual and verbal information are not entirely independent in working memory. The episodic buffer is able to account for these data by acting as a “back-up store” capable of integrating information from multiple modalities (Baddeley, 2000). Furthermore, it is this capability which allows, according to Baddeley (2000, 2012), the episodic buffer to support the creative integration of disparate forms of information when imagining episodes or scenarios (Baddeley asks us to imagine a pink elephant playing ice hockey).

It is curious then, that Baddeley and colleagues have researched the hypothesised binding function of the episodic buffer by largely investigating binding *within* the visual and verbal

domains, as opposed to visual-verbal (i.e. multimodal) binding. Within the visual domain, a number of experiments from Baddeley's lab have shown, using a dual-task procedure, that the binding of visual features is not dependent on central executive resources (Allen, Baddeley, & Hitch, 2006; Baddeley, Allen, & Hitch, 2011). Similar findings have been found for the chunking of words in sentence comprehension (Baddeley, Hitch, & Allen, 2009). These findings have led to a characterisation of the episodic buffer as a "purely passive system, but one that serves a crucial integrative role because of its capacity to bind information from a number of different dimensions into unitized episodes or chunks" (Baddeley et al., 2011, p. 1399).

It is too early to tell if the concept of the episodic buffer will prove to be a fruitful addition to Baddeley's model of working memory, although one issue with the concept stands out currently. Baddeley's theorising of the buffer as a multimodal store is not at all aided by the investigation of binding *within* modalities. It is not clear why the visuospatial sketchpad could not be the locus of bound object representations. Likewise, the binding of words into chunks seems to be a process well suited to the phonological loop. There seems to be an element of reification in Baddeley's investigations on the topic. First, he speculated that the episodic buffer was responsible for binding disparate forms of information (Baddeley, 2000). This is followed by a research program that investigates binding (Allen et al., 2006; Baddeley et al., 2009), and then this function is assigned to the episodic buffer (Baddeley et al., 2011).

The model of working memory first proposed by Baddeley and Hitch (1974) and refined over the years by Baddeley (1986, 1992, 1998b, 2000, 2007) is one of the most influential models in the history of cognitive science. In recent years, however, an alternative model of working memory has gained traction.

### **1.3. Activation Models of Working Memory**

The three storage buffers of Baddeley suggest a clear demarcation between information held in a temporary storage system and information in long-term memory. That is, working memory storage is regarded as occurring in stores or buffers distinct from long-term memory. A number of authors have, however, argued strongly against this claim (Cowan, 2001; Crowder, 1993; Fuster, 1998; Ranganath & Blumenfeld, 2005; Ruchkin, Grafman, Cameron, & Berndt, 2003). Instead, they suggest that a more parsimonious theory — and one better able to explain a range of findings — is to equate working memory with the temporary activation of long-term memory representations. In this section, I will outline evidence against the claim that working memory buffers are independent of long-term memory, as well as evidence supporting the claim that working and long-term memory tap into a single representational store.

The major evidence pointing to a distinction between working and long-term memory comes from neuropsychological studies showing a double dissociation between the two forms of memory. As mentioned earlier, a number of studies have shown that damage to perisylvian/temporoparietal cortex results in markedly decreased performance in verbal short-term memory tasks while keeping verbal long-term memory intact (Risse et al., 1984; Shallice & Warrington, 1970; Warrington et al., 1971). In addition, patients with damage to medial temporal lobe regions exhibit striking long-term memory deficits as in the famous case of HM (Scoville & Milner, 2000), while showing no such deficits in short-term memory (Cave & Squire, 1992).

Ranganath and Blumenfeld (2005) point out a few issues with interpreting these double-dissociation results as necessarily indicating a sharp distinction between working and long-term memory. While working memory is often reported as being unaffected by damage to the hippocampus and surrounding structures in the medial temporal lobe, the research showing these effects have generally used highly familiar, overlearned items (Baddeley & Wilson,

2002; Cave & Squire, 1992). On the other hand, when visual working memory is tested for novel and unfamiliar items, medial temporal lobe amnesics exhibit striking deficits in working memory tasks when a single abstract shape is maintained in working memory (e.g. Holdstock, Shaw, & Aggleton, 1995; Owen, Sahakian, Semple, Polkey, & Robbins, 1995) or a single novel face (Olson, Moore, Stark, & Chatterjee, 2006). The importance of the medial temporal lobe to working memory for novel information has been bolstered by a recent study showing that medial temporal lobe amnesics show working memory deficits for novel (non-famous) faces but not for familiar (famous) faces. In addition, the same study showed a deficit for non-words and unfamiliar, low-frequency words, but not for highly familiar words (Rose, Olsen, Craik, & Rosenbaum, 2012). These findings suggest that performance in a working memory task can be performed to a reasonable level by medial temporal lobe patients if they are able to rely on the rehearsal of activated semantic (long-term) representations stored elsewhere in the cortex. This is in many ways analogous to a phenomenon in long-term, autobiographical memory in which old memories become *semanticised* over time such that they can be accessed independently of the medial temporal lobe, while more recent (i.e. more novel) episodic memories always rely on medial temporal lobe activity (Addis, Roberts, & Schacter, 2011; Moscovitch, Nadel, Winocur, Gilboa, & Rosenbaum, 2006).

The other side of the double-dissociation coin — that damage to perisylvian regions disrupts verbal working memory and not long-term memory — is also not entirely convincing upon closer scrutiny. Ranganath and Blumenfeld (2005) make the key criticism that, in these studies, the working and long-term memory tasks differ not only in terms of the duration between study and test, but also by the type of material that has to be stored. For example, while working memory tasks require the storage of random digits (that have to be recalled in the correct sequence), long-term memory tasks often require the learning of

meaningful words via multiple learning phases. When this is controlled for (for example, when working and long-term memory are both tested using non-words), the poor performance on working memory tasks extends to long-term memory for these patients (Belleville, Caza, & Peretz, 2003). This suggests that the differences in performance in these patients for working and long-term memory tasks (e.g. Shallice & Warrington, 1970) can be attributed to an inability to maintain phonological information and a largely intact ability to maintain semantic information.

Further evidence for a representational system shared by working and long-term memory can be found in an ever-growing body of neuroimaging research showing common regions activated by both. Specifically, both forms of memory involve the reactivation (in the case of long-term memory) or sustained activation (for working memory) of regions responsible for the initial perception of a given event. In the case of the former, Wheeler, Petersen, and Buckner (2000) have shown that many of the same regions active during the perception of faces (e.g. fusiform gyrus) and sounds (e.g. superior temporal gyrus) exhibit increased BOLD signal signatures when engaging in vivid remembering of these stimuli, even when the memory phase occurred a day after the encoding phase. A recent study using MVPA has further highlighted the intimate link between perception and long-term memory (Buchsbaum, Lemire-Rodger, Fang, & Abdi, 2012). The study consisted of three phases: in phase 1, participants were presented with novel videos in an fMRI scanner; in phase 2, which lasted 2-3 months, the same participants practised “mentally replaying” the videos; in phase 3, they were returned to the scanner and had to replay the videos in their mind. Two analyses of relevance were performed for this study. First, a number of regions were shown to be conjointly active for the perception and recall of individual videos. In addition, MVPA was used to train a classifier to reliably classify, on the basis of patterns of activation measured during phase 1, neural patterns in phase 3. That is, using neural patterns from the perception

phase, the classifier was able to determine (with high accuracy) which video a participant was remembering based on neural patterns measured in phase 3.

Similar findings emerge from the neuroimaging literature on working memory, which shows that working memory maintenance does not involve the transferring of information into specialised buffers in the frontal lobe — as suggested by many authors (Courtney, Petit, Haxby, & Ungerleider, 1998; Courtney, 2004; Goldman-Rakic, 1987) — but instead arises from the sustained activation of stimulus-specific, posterior regions of the brain. For example, Ruchkin and colleagues (2003) review evidence showing sustained ERP deflections in these regions during working memory tasks. In addition, source localisation showed that maintaining spatial information resulted in sustained activity within the dorsal stream (parietal-occipital junction), while the ventral stream (anterior temporal cortex) is responsive to object information. fMRI work has shown that fusiform and parahippocampal regions show sustained BOLD responses to the maintenance of faces and houses respectively (Ranganath et al., 2004).

While the imaging results described above are *prima facie* evidence for a representational system common to working and long-term memory, this interpretation is potentially guilty of committing a form of the reverse inference fallacy, which involves inferring a cognitive process based on some pattern of neural activity. The most glaring examples of this error of reasoning can be found in the burgeoning field of neuromarketing, which has produced results claiming to show, for example, that iPhone owners “love” their phones (Lindstrom, 2011), not because of any behavioural evidence, but because presenting images of iPhones resulted in activation of the insular cortex. This misinterpretation relies on the fact that, since previous work has (tenuously) linked the insula with love (Bartels & Zeki, 2000), the insular activation in the iPhone study can also be attributed to such feelings. The problem, of course, is that there is no faithful one-to-one mapping between cognitive processes and neural

regions (Poldrack, 2006). An ironic example pointing to this fact is research highlighting the role of the insular cortex in the neural network underlying feelings of hate (Zeki & Romaya, 2008). Similarly, it is a reverse inference to claim that working memory involves activated long-term memory representations based on working memory imaging studies that show the activation of brain regions known to be involved in long-term memory.

To address this issue, Lewis-Peacock and Postle (2008) performed an elegantly designed experiment to directly investigate the link between the two memory systems. In a 3-phase experiment, the authors used MVPA to assess whether the neural patterns evoked by the activation of long-term memories could be used to predict the contents of working memory. In the first phase, participants were presented with images of familiar objects, faces and locations in the scanner and required to make a like/dislike judgement for each stimulus. The evaluation of each stimulus is important as it relies heavily on episodic and/or semantic memory. In the second phase, a subset of the images was used to create six pairings and participants learned the associations between these images outside the scanner. Finally, they returned to the scanner and performed a delayed paired-associate recognition task. In this task, an image from phase 2 is presented and participants have to maintain the associated image that they learned in the previous phase in working memory. After a delay period of 11 seconds, a probe was presented and participants had to respond whether it matched the associated image. The MVPA analysis involved the training of a classifier on the data from phase 1 (the long-term memory task) to distinguish between faces, locations and places. Next, that same classifier was used on the data from phase 3 (the working memory task) and was able to reliably determine the contents of working memory (face, location or object) based on patterns of activity generated in the long-term memory task. This finding provides direct evidence that working and long-term memory both involve the activation of a single underlying neural workspace.

While the findings discussed in this section are difficult to reconcile with the notion of specialised buffers which maintain information independently of perception and long-term memory, they are compatible with two aspects of the Baddeley model. First, activation models of working memory agree that working memory is organised in a modular fashion, such that visual and verbal information are independently maintained in working memory (Slotnick, 2004). Second, activation models also posit a central executive. In these models, the role of the central executive is to orient attention to the task-relevant long-term memory representations resulting in their activation (Cowan, 1999, 2001).

#### **1.4. Visual Working Memory**

In this section, I narrow the focus from general theories of working memory to the specific topic of visual working memory. The recent explosion of research into visual working memory has brought with it a number of intense debates in the literature concerning two issues: the capacity of visual working memory and the nature of visual working memory representations. Both of these issues have their (modern) genesis in the publication of a highly influential paper by Luck and Vogel (1997). Given this study's influence, it pays to examine their series of experiments in some detail.

First, the authors employed a “one-shot” change-detection task in which participants were presented with an array of 1-12 coloured squares for 100ms that had to be maintained in working memory. After a 900ms delay, a second array was presented that was either identical to the initial display or differed such that one of the squares changed colour, and participants were to respond accordingly (i.e. make a same-different judgement). Using the formula<sup>3</sup> proposed by Pashler (1988) the authors approximated working memory capacity to four

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<sup>3</sup>  $K = N \times (H - F)$ , where  $K$  is capacity,  $N$  is the set size of the memory display,  $H$  is hit rate and  $F$  is the false alarm rate.

items. Importantly, this was also the case when the impact of verbal working memory was minimised by requiring participants to maintain and rehearse a 2-digit number in working memory throughout the trial.

To rule out the possibility that visual working memory storage capacity was underestimated due to a lack of encoding, the authors then extended the duration of the initial display presentation to 500ms and found that the same measures of capacity emerged. While this precludes the contribution of encoding processes to their results, it is still possible that performance drops off sharply as set size increases not only because of storage limits, but because an increase in set size is necessarily accompanied by an increase in the number of decisions made during the comparison phase of the task. The contribution of decision processes to performance was assessed by cueing an individual item in the test display. This ensured that a single decision was required at all set sizes. This manipulation still produced capacity estimates of approximately four items, providing compelling evidence that this estimate can be attributed solely to working memory storage.

Next, the authors measured capacity for the visual features of colour and orientation using rectangular bars as stimuli that varied by these two feature dimensions. They found no difference in performance between the two; again the capacity estimates for both visual features approximated to four items. Colour and orientation trials were blocked separately in this experiment; as such, this finding does not speak to whether visual working memory stores integrated objects or visual features. A third “conjunction” condition was added to the experiment in which either orientation or colour could change. Interestingly, performance in this condition was no different to the single feature conditions suggesting that visual working memory capacity is constrained solely by the number of objects independently of the visual feature load. For example, maintaining eight visual features across four objects (as in the

conjunction condition) produced equivalent performance as maintaining four features across four objects (as in the single feature conditions).

This was extended in an experiment that doubled the number of visual features to four by using rectangular bars as stimuli defined by the presence or absence of a gap, size (small or large), colour and orientation. As with the previous experiment, there were four single feature blocks, in which participants had to detect changes along a single visual feature dimension (see [Figure 1.1](#)). In addition, a critical conjunction block was presented where a change could occur along any of the four feature dimensions. Strikingly, performance was equivalent across all single feature conditions as well as the conjunction condition. To continue with the previous example, this suggests that maintaining 16 visual features across four objects is no different to the maintenance of four features across four objects.

Parsimony suggests that the representational format best equipped to deal with these findings consists of a single visual working memory store that maintains integrated objects. Furthermore, object capacity is unaffected by the informational complexity of each item. Luck and Vogel (1997) liken this to the “chunking” process commonly observed in verbal working memory (Miller, 1956): the number of bits (visual features) in each chunk (object) is negligible in determining working memory capacity. An alternative explanation for the similar performance in single feature and conjunction conditions is that each visual feature is maintained in an independent store or channel. In this framework, an increase in the total number of visual feature values in the conjunction condition does not result in a performance decrement because they are distributed evenly across the different visual feature dimensions<sup>4</sup>. For example, while 16 visual features need to be maintained in a conjunction trial when the

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<sup>4</sup> Even though a feature channel account can also readily explain equal performance for conjunction conditions compared to single feature conditions, this finding is often incorrectly interpreted as strong evidence for an object account of visual working memory representation (e.g. Ko & Seiffert, 2009; Landman, Spekreijse, & Lamme, 2003)

set size is four items, these could be maintained across four feature stores such that each feature store holds four visual feature values. In a single feature trial, the number of visual feature values in the relevant feature store is also four (given a set size of four). In other words, for any given set size the number of feature values in a feature store is never greater in a conjunction trial than a single feature trial. As such, accuracy is equivalent in these two types of condition.

To distinguish between the integrated object and feature channel accounts, Luck and Vogel (1997) performed a critical experiment using stimuli that were defined by two visual feature values belonging to the same visual feature dimension. Specifically, the stimuli in the conjunction condition were bi-coloured squares that contained a small square of one colour surrounded by a larger square of another colour. As control conditions, the stimuli were single coloured squares that were either large or small (see Figure 1.1.). If visual features are the “building blocks” of visual working memory, then performance should be dictated by the number of colours in the initial display and not by the number of objects i.e. accuracy in the conjunction condition should be lower than for both the single colour conditions. As in the previous experiments, however, performance in the conjunction condition was equivalent to the single colour conditions, providing strong evidence that the fundamental unit of visual working memory is the integrated object (and not visual features).

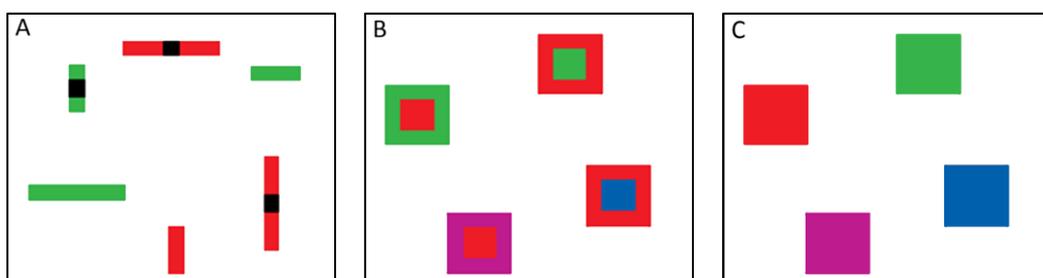


Figure 1.1. A schematic of selected memory displays described in Luck and Vogel (1997). A shows their “quadruple conjunction” condition, in which a change could occur on any of four visual features (size, orientation, colour and the presence/absence of a gap”. B shows their bi-coloured squares, which produced equivalent performance to single coloured squares (the “large square” variant of this is shown in C).

In summary the findings of Luck and Vogel (1997) can be reduced to two central claims: visual working memory capacity is approximately four items, and the fundamental units of visual working memory are integrated object representations. What follows is a summary of current positions in the literature on these two issues.

#### **1.4.1. The Capacity of Visual Working Memory**

One of the fundamental questions in visual working memory research is how to best characterise its capacity limits. While there were earlier investigations on this issue (e.g. Brener, 1940), these studies were confounded by the potential use of verbal working memory to aid performance. Luck and Vogel (1997) minimised the contributions of verbal working memory and, in a series of change-detection tasks, proposed the capacity of visual working memory to be about four items. Recently, however, a number of studies have questioned whether change-detection tasks consistently underestimate the true capacity of visual working memory.

The common element in these studies is the use of an informative retroactive cue (retro-cue hereafter) presented in the delay period of change-detection tasks. These cues serve the function of informing the participant which item (held in memory) could potentially change i.e. change trials always involve a change to the cued item. Landman, Spekreijse, and Lamme (2003) showed that presenting a cue at any stage during the delay period (from 300 to 1500ms after the offset of the initial display<sup>5</sup>) led to a marked increase in capacity estimates of visual working memory. While the “no cue” condition produced capacity estimates of

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<sup>5</sup> The fact that this effect occurs robustly across all these ISIs (and not just at ISIs less than ~500ms) shows that this effect cannot be attributed to iconic memory processes, which has a duration of approximately 300ms (Sperling, 1960b)

about four items and matched those of Luck and Vogel (1997), a retro-cue increased these estimates to approximately seven items. To assess whether this effect is due to a reduction in the number of decision processes in the retro-cue conditions, the authors included a condition with a post-cue (a cue presented simultaneously with the test display). This manipulation had no effect and performance was almost identical to the no-cue condition. Instead, the substantial drop in capacity estimates between the retro-cue and no-cue conditions suggests a visual working memory capacity much larger than four items. In addition, only a subset of working memory representations survives the interference produced by the test display in change-detection tasks.

Sligte, Scholte, and Lamme (2008) extended these findings and developed a tri-partite model of visual working memory. That is, they proposed that retro-cues tap into an intermediate stage of visual working memory between iconic memory and a durable working memory. This intermediate store is proposed to have two qualities that distinguish it from visual working memory: it has a substantially higher capacity, as shown by capacity estimates of up to 16 items in their study; representations housed in this store are particularly fragile and are prone to interference from subsequent perceptual input. This interpretation of retro-cue findings was strengthened by an experiment using TMS and fMRI that assessed the relative contribution of dorsolateral prefrontal regions during retro-cue and post-cue change detection trials. First, participants performed a standard change-detection task in the scanner that allowed the authors to determine the DLPFC coordinate exhibiting the highest BOLD response in each participant. Next, participants performed a change-detection task containing either a retro-cue or a post-cue. In addition, on 50% of trials participants received a TMS pulse 600ms after the initial display that was centred on the DLPFC location previously determined by each participant's individual fMRI activation. The results showed that TMS pulses affected performance for post-cue trials but failed to significantly impact performance

in the retro-cue trials. Sligte and colleagues (2011) interpreted this finding as evidence that visual working memory and fragile visual working memory recruit different neural regions: specifically, they argue that the DLPFC plays a vital role in visual working memory maintenance (as tested by the post-cue trials), while the fragile, intermediate visual working memory store is not dependent on DLPFC activity.

While many other studies have found that retro-cues modestly benefit performance in change-detection tasks (e.g. Griffin & Nobre, 2003; Makovski & Jiang, 2007; Makovski, Sussman, & Jiang, 2008; Matsukura, Luck, & Vecera, 2007), some authors have challenged the proposal that this necessarily indicates an additional, high-capacity visual working memory buffer. First, as noted by Matsukura and Hollingworth (2011), the retro-cue benefits observed in Sligte et al. (2008) exceed those commonly reported in other studies, that generally fail to show retro-cue conditions producing performance that exceed four items<sup>6</sup>. Specifically, Sligte and colleagues report that a retro-cue coupled with a test display of 32 horizontally or vertically aligned rectangular bars results in capacity estimates of approximately 16 items. This estimate is, however, almost certainly an artefact of the particular nature the rectangular bars were organised in the memory display of this study, such that co-linear bars could easily have been grouped into higher-order perceptual units. When this strategy was prevented, capacity estimates drastically dropped to 5-6 items (Sligte et al., 2008). Furthermore, the methodology of Sligte and colleagues' study involved two unusual aspects. First, their study included a three hour practice session on the day before the experiment. In addition, Sligte personally communicated to Matsukura and Hollingworth

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<sup>6</sup> Sligte et al. (2008) measure performance using  $K$ , a measure of visual working memory capacity (see footnote 2), while most studies showing a small (but significant) retro-cue benefit have generally reported percent or proportion correct. Assuming an even number of change and no-change trials, conversion of proportion correct to  $K$  is relatively straightforward using the formula:  $K = N \times (2p - 1)$ , where  $N$  is set size and  $p$  is proportion correct. When this is applied to other retro-cue studies, the benefits in  $K$  are generally below 1 item, strikingly fewer than the retro-cue benefit of up to 8 items in Sligte et al. (2008).

(2011) — but failed to report in Sligte et al. (2008) — that a participant was able to repeat any experimental blocks that fell below his/her expectations. Given these extensive training effects, it is no surprise that capacity estimates were particularly high in Sligte et al. (2008). Similarly, the estimates reported by Landman et al. (2003) are likely to be inflated by practice effects as their participant pool contained what are described as “experienced observers”. Indeed, Matsukura and Hollingworth (2011) attempted to replicate the findings of Sligte et al. (2008) but only attained such high capacity estimates when participants were submitted to a three hour practice session.

In addition to being a very high-capacity system, the intermediate visual working memory store of Sligte et al. (2008) is posited to contain highly fragile representations, such that they are particularly sensitive to visual interference. This has, however, recently been challenged by Makovski (2012) who has shown that a retro-cue benefit still exists when visual interference is presented to participants between the initial display and the retro-cue. This finding, in conjunction with the methodological flaws of Sligte et al. (2008) that inflated the capacity estimates of that study, renders untenable the notion of a high-capacity, fragile visual working memory store. Instead, the modest increase in change-detection performance for retro-cue conditions is likely explained by two processes. First, the retro-cue allows participants to orient attention to the relevant item in working memory (Griffin & Nobre, 2003; Lepsien, Griffin, Devlin, & Nobre, 2005; Lepsien & Nobre, 2007). Second, the cued item is protected from degradation (as opposed to merely being prioritised for comparison), while uncued items undergo a more rapid rate of degradation in working memory (Matsukura et al., 2007).

The retro-cue paradigm has generated a great deal of debate regarding capacity of visual working memory; implicit in this debate is the assumption that visual working memory capacity is constrained solely by the number of available “slots”. This view has, however,

been challenged in two different ways. First, Alvarez and Cavanagh (2004) have reported that performance in change-detection tasks — an index of visual working memory capacity — is strongly modulated by the informational complexity of the maintained stimuli. Alvarez and Cavanagh (2004) used a visual search task to assess the informational complexity of a range of stimuli — the assumption being that those stimuli types containing more information or visual detail should result in longer search times. These stimuli classes were then used in change-detection tasks and results showed that the visual search rates for different stimuli types almost perfectly predicted performance in change-detection tasks ( $r^2 = .992$ ), with coloured patches producing the fastest visual search times and highest capacity estimates, followed (in ascending order of visual search response times and descending order of visual working memory capacity) by letters, Snodgrass line drawings, Chinese characters, random polygons and shaded cubes. This finding suggests that visual working memory capacity is best captured by the equation  $C = I \times N$ , where  $C$  is a fixed-capacity resource,  $I$  is the informational load of each item and  $N$  is the maximum number of items able to be maintained in visual working memory. That is, the capacity of visual working memory (in terms of the number of items able to be maintained) is contingent on the amount of information or visual detail inherent in each item. Alvarez and Cavanagh (2004) further argue that while visual working memory capacity is determined in part by the informational content of items, there still exists an upper limit of the number of items that can be maintained. Specifically, they claim that visual working memory has an upper limit of about five items, even for stimuli with very little visual detail. This was inferred by extrapolating the regression line mapping the relationship between capacity and visual search rates to show that when the visual search rate approaches zero, capacity estimates are about five items.

It should be noted, however, that visual search response times need not necessarily be an index of visual complexity. Awh, Barton, and Vogel (2007) have argued that it is in fact

inter-item similarity driving both the visual search and change-detection performance in the experiments by Alvarez and Cavanagh (2004). First, Awh and colleagues (2007) replicated the high correlation between visual search response times and change-detection performance across the same stimuli classes as Alvarez and Cavanagh (2004). They then proceeded to tease apart the effects of visual complexity and visual similarity by performing a change-detection task requiring the maintenance of two classes of high-information visual stimuli: random polygon characters and shaded cubes. Furthermore, two types of changes could occur: *within-category* changes (e.g. a cube changing to another cube) and *across-category* changes (e.g. a cube changing to a polygon). The authors reasoned that if informational complexity was the limiting factor in change-detection performance, then these two types of changes would produce similar patterns of performance. If, however, item-similarity drives performance then the across-category conditions should produce significantly better performance than the within-category condition. This is exactly what the authors found, prompting them to argue that visual working memory is limited solely a fixed number of slots, but that change-detection performance is strongly modulated by potential errors at the comparison phase of the task such that detecting changes between highly similar items is more difficult than for dissimilar items.

Others have argued against slot models from a signal detection perspective that emphasises the role of noise in working memory representations. According to this view, performance drops steeply in change-detection tasks as set size increases because set size correlates with the amount of noise associated with each working memory representation. In other words, as set size increases, the precision (or resolution) of maintained items decreases due to an increase in internal noise. Others have characterised this position as a “resource model” of visual working memory, in which a resource is shared amongst the items in

working memory such that the precision of each item is inversely related to the number of maintained items (Bays, Catalao, & Husain, 2009; Bays & Husain, 2008).

In a series of change-detection experiments requiring the maintenance of colour, orientation or spatial frequency (each tested separately), Wilken and Ma (2004) compared slot models (high-threshold models in their terminology) with signal detection models and found strong support for the latter. These two types of models predict very different receiver operating characteristics (ROCs), with high-threshold models predicting ROCs characterised by straight lines and signal detection threshold models predicting curved, bow-shaped ROCs. In one set of experiments, Wilken and Ma varied set size while in another set they kept set size constant and varied the number of items that change in the test display. In both sets of experiments, a high-threshold model failed to provide a good fit for the observed ROCs, while signal detection models provided.

In addition, Wilken and Ma then performed a final set of experiments that varied set size but required a different response to the simple yes/no judgements necessary in change-detection tasks. In these experiments, instead of a second array being presented at test, memory was probed using a location cue (indicating which item in memory was being tested) and participants were required to indicate the relevant feature at that location. Importantly, responses were made on a continuous scale such that the precision of the maintained items could be assessed. For example, in the colour experiment, participants were presented with a colour-wheel and had to select a location on the colour wheel that most closely resembled the colour of the cued item. High-capacity models predict that the variability of judgement errors should not vary with increasing set-sizes when the set-size is below visual working memory capacity. For higher set-sizes, however, variability should increase substantially as participants make random guesses for those items that do not “fit” in working memory. The results showed that, for all visual features tested, the variability of errors increased linearly

with set-size, even for those set-sizes well below the traditional estimate of visual working memory capacity (i.e. 4 items). This is in accordance with the hypothesis claiming that as set-size increases, representations in working memory become more noisy and less precise. In addition, it is strong evidence against slot models of working memory that regard visual working memory representations to be “high-resolution” and maintained in an all-or-none fashion.

The subsequent work in this paradigm has largely centred on the appropriate statistical analyses and interpretations of results. For example, Zhang and Luck (2008) pointed out the results of Wilken and Ma (2004) are also amenable to slot models of working memory. Specifically, it could be the case that when the set-size is below working memory capacity, a single item may be represented in more than one slot in working memory. For example, when the set-size is one item, this single item could be represented four times in working memory, with each slot maintaining an independent representation of the item. In addition, during the response phase, participants may average across the slots resulting in high estimates of precision. If this view is correct, then precision should decrease as set size increases even when the set-size is below working memory capacity.

Zhang and Luck (2008) replicated the methods of Wilken and Ma (2004) and reported results that support slot models of visual working memory. The authors teased apart the effects of two types of trials: ones in which participants correctly recall the probed item and select a value on the colour-wheel close to that of the probed item, and trials in which the probed item is not available in working memory and participants guess randomly. From this mixture of responses, Zhang and Luck were able to derive two independent measures: one that estimated the probability an item was maintained in visual working memory, and another that estimated the precision with which the item was maintained. Their results strongly supported slot models, as the probability that an item was maintained in working memory

stayed relatively constant for set-sizes one, two and three, but dropped sharply when the set-size was six items. In addition, Zhang and Luck (2008) performed an experiment that inserted valid, neutral or invalid retro-cues between the initial display and recall phase of the task. The results generally supported slot models and showed that validly cueing an item in working memory lead to an increase in the number of slots devoted to representing that item.

An implicit assumption in the work of Zhang and Luck (2008), is that performance in their colour-wheel recall task is dependent solely on the precision of the cued item's colour in working memory. As noted by Bays et al. (2009), however, the use of a spatial cue introduces the likelihood that responses are also affected by variability in memory for locations. If this is the case, then in addition to correct trials and random guesses modelled by Zhang and Luck, there should be a proportion of trials in which participants respond with a colour value close to one of the uncued items. That is, the appropriate mixture model for this paradigm requires separating the proportion of three types of trials: target trials (where the selected colour value is close to the cued item's colour), non-target trials (the selected colour is close to an uncued item's colour) and random guesses. Bays et al. showed that, when these non-target trials are accounted for, the pattern of results provide no evidence for slot models of working memory. First, the number of non-target responses increases with set-size (suggesting that the precision of location information decreases with set-size). Second, the proportion of random guesses was far below what would be expected if slot models were correct (a set-size of 6 items resulted in only ~10% of random guesses).

The issue of working memory capacity is multi-faceted, with many independent debates currently being played out in the literature. It is interesting to note, however, that visual working memory capacity — whether it be defined as a resource or a fixed number of slots — is not taxed even in situations in which maintaining as much visual information in working memory may seem useful. For example, in a number of experiments using a block-

copying paradigm, Ballard, Hayhoe, Pook, and Rao (1997) asked subjects to duplicate a particular spatial arrangement of coloured blocks while their eye and hand movements were tracked. The results of these experiments showed that subjects made far more eye movements than would be expected if they were using working memory to its maximum capacity. Often, subjects would perform a saccade from the model to the block resource area, select a block, perform a saccade back to the model, and then to the assembly area before dropping the block in the correct location. Ballard et al. suggest that the saccade back to the model after the block has already been selected suggests that this saccade serves the purpose of retrieving the block's spatial location from the model, with the block's colour already retrieved (and possibly now discarded from working memory) in the first fixation of the model. They suggest that this minimal memory strategy is preferred because of the high cost of maintaining items in working memory<sup>7</sup>. These findings are in accord with theories that explain the low capacity of visual working memory — and presumably our (unconscious?) reluctance to use this capacity to its full effect — by invoking the notion of a stable, external “world as an outside memory” (O'Regan & Noë, 2001, p. 945).

#### **1.4.2 The Units of Visual Working Memory: Objects or Features?**

In addition to proposing a fixed number of available slots in visual working memory, Luck and Vogel (1997) made the related claim that the “building blocks” of visual working memory are integrated object representations. That is, stored in each slot in visual working memory is a single, multi-dimensional code that represents all of the visual features associated with a remembered item (Figure 1.2 b). An alternative view — and one championed in the current thesis — is that visual working memory maintains information in a distributed manner across multiple stores or channels, each specific to a given visual feature

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<sup>7</sup> This discussion of Ballard et al.'s work is taken directly from Colling and Roberts (2010)

dimension (Figure 1.2 c). According to this view, the associations between visual features are also maintained in visual working memory, but they constitute representations additional to the representations of visual features. This view is sometimes referred to as the *weak-object hypothesis* (Olson & Jiang, 2002), and is similar in many respects to the “*hierarchically structured feature bundles*” proposed by Brady, Konkle, and Alvarez (2011).

Relevant to this debate is the relationship between the *perceptual* processing of features and objects — a topic with a long history in cognitive science, with fundamental contributions from the domains of experimental psychology and neuroscience. The picture that has emerged from this research is one in which visual features are initially registered independently in distinct cortical sites (Tootell, Dale, Sereno, & Malach, 1996). The binding of visual features into a higher-order object representation requires the allocation of attention to the object’s location (Treisman & Gelade, 1980; Treisman, 1996, 1998). This allocation of attention to a location of space generates the creation of an object file: a representation that binds together the visual features associated with a given item (Kahneman, Treisman, & Gibbs, 1992). Importantly, object files have the property of being updateable. That is, when an object moves through space or changes in some way, the corresponding object file is updated, thereby enabling the successful tracking of objects across the visual field.

The object file theory is similar in many respects to the indexing theory proposed by Pylyshyn (1989, 1994, 2001), which proposes that a limited number of objects are pre-attentively registered by the visual system based on their spatial location. The fundamental distinction between these representations and object files is that the indices of Pylyshyn do not at any stage represent the visual features of individual items. Instead, they merely “point to” objects in the visual field, and subsequent (attentionally mediated) processes are required to assign visual features to each item. On the other hand, while object files are primarily

defined by spatiotemporal information, visual feature information is able to be later added to the file (Kahneman et al., 1992; Leslie, Xu, Tremoulet, & Scholl, 1998; Scholl, 2001).

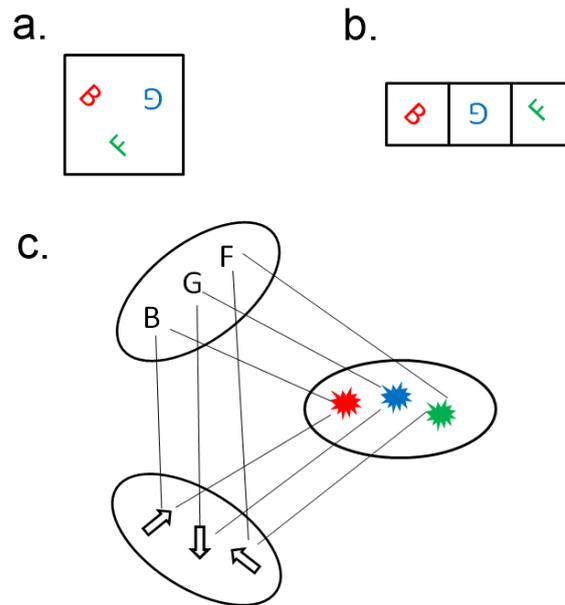


Figure 1.2. A given memory display (a) could be represented either as integrated objects in distinct slots (b), or as a collection of visual features bound together by associative links (c).

Object-based theories of visual working memory propose that the representations maintained in working memory closely resemble object files. As mentioned earlier, Luck and Vogel (1997) showed that maintaining bi-coloured items in working memory comes at no cost in performance relative to the maintenance of single-coloured squares, suggesting strongly that visual working memory maintains integrated object representations. This critical finding has, however, failed to be replicated by three separate research groups who have shown that performance in the bi-coloured square conditions is lower than conditions in which squares contain a single colour (Delvenne & Bruyer, 2004; Olson & Jiang, 2002; Wheeler & Treisman, 2002).

A related line of evidence for object-based accounts of working memory is found in research showing an “object-based benefit” — the increase in change-detection performance when visual features are conjoined in multi-dimensional items instead of being distributed across single-feature items (Olson & Jiang, 2002; Xu, 2002). For example, performance is better when four orientations and four colours are presented in four objects (*conjunction* conditions) than when the eight visual features appear in eight different items (*disjunction* conditions) — see [Figure 1.3](#). While this finding has generally been interpreted as supporting object-based accounts, it is also possible that the cost associated with disjunction trials is compatible with feature-based accounts of visual working memory. Instead of change-detection tasks, Fournie, Cormiea, & Alvarez (2012) used a cued-recall paradigm for conjunction and disjunction trials. Responses were made using by selecting values on circular colour and orientation wheels. In the disjunction trials, two items were cued (one orientation item and one colour item — see [Figure 1.3](#)), and participants were required to respond with the associated visual feature value for each item. On conjunction trials, a single item was cued and participants had to recall both the orientation and colour associated with the cued item. The value of such a design is that it tests for an object-based benefit while simultaneously allowing for the direct assessment of the degree of feature integration in working memory. The findings showed an increase in performance for conjunction trials, supporting previous work showing an object-based benefit. However, there was no evidence for object-based accounts of working memory, as analysis of the responses showed that, contrary to the proposal that representation of an object is all-or-none, colour and orientation information were lost independently of each other. The independent failing of visual features reported in this study has also been shown in other studies using the same cued-recall paradigm for multi-feature items (Bays, Wu, & Husain, 2011; Fournie & Alvarez, 2011). This finding — that the object-based benefit does not necessarily entail the maintenance of

integrated object representations — highlights the need to investigate directly the binding of visual features in working memory. Specifically, to show that visual working memory maintains integrated objects, it needs to be shown that memory for individual visual features is equivalent to memory for the associations between visual features.

Wheeler and Treisman (2002) performed a series of change-detection tasks that directly compared visual working memory for these two forms of visual information. The memory stimuli in their experiment were coloured shapes, and the critical conditions were *2-feature* and *binding* conditions. In the former, either colour or shape could change between initial and test displays, while in the latter two shapes swapped colours (see Figure 1.4). The two conditions were matched in that they both required the encoding and maintenance of shape and colour information, but only the binding condition requires that participants maintain the associations between each shape and colour. The results showed that participants exhibited the poorest performance in the binding conditions.

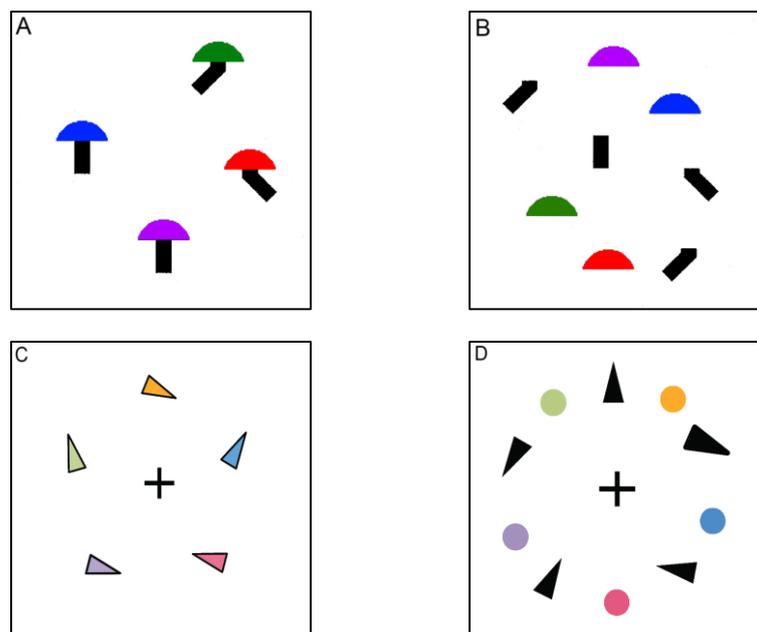
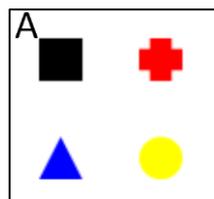


Figure 1.3. Example memory displays showing two versions of conjunction and disjunction trials. A and B are modified from Xu (2002); C and D from Fougne et al. 2012.

Interestingly, this binding deficit was only apparent when the test display contained multiple items. Using a single probe at test resulted in no difference between 2-feature and binding conditions. To determine if this discrepancy in findings was due to an increase in the number of decisions required for multi-item test displays, Wheeler and Treisman (2002) performed a version of the task in which a single item was cued in a multi-item test display, and participants were required to make their decision based on only the cued item (“Has this item changed?”). This manipulation did not result in increased performance, however, suggesting that the binding deficit cannot be attributed to decision processes associated with multi-item test displays. Wheeler and Treisman (2002) proposed that these displays disrupt binding in visual working memory as they recruit attention. According to this proposal, binding information is maintained in working memory by allocating attention to working memory representations. When attention is diverted away — as in the case of multi-item test displays, but not so for single-item test displays — binding information is lost from working memory. Memory for visual feature information, on the other hand, remains largely intact allowing for greater performance in 2-feature conditions relative to the binding condition when multiple items are presented at test. There is, however, scant evidence for this proposal as subsequent studies have failed to show that attention plays a role in maintaining binding information in visual working memory (Allen et al., 2006; Delvenne, Cleeremans, & Laloyaux, 2010; Johnson, Hollingworth, & Luck, 2008; Yeh, Yang, & Chiu, 2005, but see Fournie & Marois, 2009).



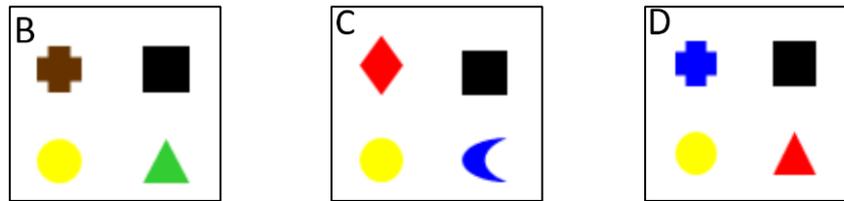


Figure 1.4. A shows an initial display similar to those used by Wheeler and Treisman (2002). In the *2-feature* condition, two items could change colour (B) or two items could change shape (C) in the test display. In the *binding* condition, two shapes swapped colours (D).

Another paradigm that has been used to investigate the issue of binding in visual working memory is the multiple object permanence tracking (MOPT) paradigm (Alvarez & Thompson, 2009; Saiki & Miyatsuji, 2007; Saiki, 2003a, 2003b). In these tasks, items are presented in a circular array and all move at a constant angular velocity. In addition to the memory items, displays contain a stationary “windmill-shaped” object that ensures the items are occasionally occluded during their circular motion. While the particulars of each study vary, the basic task in these experiments is to detect whether any of the items change while occluded. The results from these studies overwhelmingly show that feature bindings fail readily in working memory compared to memory for individual visual features.

In summary, a great deal of behavioural evidence exists — from change-detection tasks, cued-recall tasks and MOPTs — suggesting that the representational format of visual working memory involves visual features being stored independently, with additional representations coding the association between feature channels. In addition, this binding information seems more prone to representational failure than visual feature representations.

### **1.5. The current thesis**

In Chapter 2 of this thesis, I extend on findings that have shown that the representational failure of binding information can occur independently of visual feature storage in working

memory. This was achieved by using a modified version of the change-detection task reported by Wheeler and Treisman (2002). The findings of the latter study have been questioned in two respects<sup>8</sup>. First, Allen et al. (2006) noted that Wheeler & Treisman's (2002) results could have been confounded by the adoption of a specific strategy for performing the task in the binding condition when the test display is a single item. When there is a change in this condition, participants have two independent routes to the correct response. They may note that the shape in the test display is no longer the same colour as in the initial display. Alternatively, they may note that the colour presented in the test display was originally paired with another shape. Such a strategy is not available when changes involve the introduction of novel visual features. This is important as the equivalent performance in novel feature and binding conditions for single-item test displays is evidence that the associations between visual feature dimensions are maintained in working memory.

The results from the multi-item test displays suggest that these associations are preferentially lost from working memory. Johnson and colleagues (2008) have, however, cast doubt on these findings. The authors point out that while Wheeler and Treisman (2002) found a main effect of condition, with the binding condition producing the worst performance, it is not clear if detecting binding changes is more difficult than detecting both novel shape and novel colour conditions. That is, the necessary pair-wise comparisons were not performed. Johnson et al. repeated the experiment and found that the detection of binding changes was not worse than the detection of novel shape changes, even though it was worse than novel colour changes.

The manipulations introduced to the change-detection task in chapter 2 seek to resolve these issues. First, the degree of feature binding in working memory prior to the presentation

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<sup>8</sup> These are discussed briefly here, but elaborated on in the introduction to chapter 2.

of a multi-item test display was assessed by introducing informative retro-cues between the initial and test displays. Second, when an item was not cued in working memory, the extent of representational failure for shape, colour and binding information was determined by performing the necessary pairwise comparisons. Another difference between this task and those performed by Wheeler and Treisman (2002) and Johnson et al. (2008) is that entirely novel locations were used for the test display. This is important as location has been shown to play an important role in the initial formation of feature bindings in working memory (Treisman & Zhang, 2006).

In chapter 3, I employ a novel version of a two-alternative forced choice (2AFC) task to investigate these issues. Makovski, Watson, Koutstaal, & Jiang (2010) have used 2AFC tasks to investigate visual working memory capacity, but this paradigm has not been used in the study of binding in visual working memory. Responses in this task were made by moving the mouse cursor to the selected item, which also allowed for analysis of the trajectory of responses in different conditions. Comparing accuracy and the trajectories of responses between binding and novel feature conditions informs our understanding of the representational format of visual working memory.

While chapters 2 and 3 seek to determine whether there is a difference in performance between novel feature and binding conditions (a binding deficit) using two different paradigms, chapter 4 asks the question: what is the source of the binding deficit? That is, while chapters 2 and 3 verify the existence of a psychological effect, the contribution of chapter 4 is to outline the underlying mechanisms driving this effect. Wheeler and Treisman (2002) suggested that attentional processes contribute to the binding deficit, but this proposal has largely been discredited by later research (e.g. Johnson et al., 2008). Allen et al. (2006) proposed that binding information is particularly susceptible to visual interference, independent of attentional processes. That is, while binding information is maintained in

working memory, these representations are fragile and are easily lost upon subsequent visual input. Chapter 4 investigates whether the specific source of this visual interference is related to the *perceptual* binding of visual features.

## **Chapter 2: Study 1 – The degree of feature binding in visual working memory before and after the presentation of a test display in a change-detection task**

### **2.1 Introduction**

While investigations into the nature of representations involved in visual perception have a long history in cognitive psychology (e.g. Marr, 1982; Treisman & Gelade, 1980), there has recently been a surge of interest in the format in which items are stored in visual working memory (e.g. Bays et al., 2011; Brady et al., 2011; Fougnie, Asplund, & Marois, 2010; Luck & Vogel, 1997; Wheeler & Treisman, 2002). Research into the neural substrates of visual perception has shown that distinct cortical areas are responsible for processing different visual features, such as colour, motion, form, etc. (Grill-Spector & Malach, 2004). According to feature integration theory, attention is required to bind the visual features of a single object together (Treisman & Gelade, 1980). Once attention has been allocated to a location in space, an “object file” — a complex, integrated representation of all the visual features present at that location — is constructed, which is continually updated as the corresponding object moves through space and/or changes physical characteristics (Kahneman et al., 1992). It is possible that working memory automatically maintains representations in the same format, as integrated wholes (e.g. Luck and Vogel, 1997). Alternatively, the feature-channel account proposes that visual working memory could be stored within separate visual feature channels, with additional representations or processes responsible for maintaining binding information i.e. the associations between visual feature dimensions (e.g. Wheeler and Treisman, 2002). This debate is the central issue addressed by the experiments described in this chapter.

The most common paradigm for assessing this question is the change-detection task. A typical trial in this paradigm involves three stages. First, an *initial display* composed of a number of items is presented to the participant, who needs to encode and maintain the items

in visual working memory. This is followed by a *delay period* requiring the sustained maintenance of the initial display items in working memory. Finally, a *test display* is presented, which is either the same or different to the initial display and requires the participant to respond accordingly. Change-detection tasks come in two varieties, depending on the nature of the test display. In whole-display change-detection tasks, set size is common between the initial and test displays, with one or two items changing between initial and test displays in *different* trials. In the single-display version, only a single item is presented in the test display that may or may not match any item from the initial display.

This paradigm has been used in two different ways to shed light on the issue of binding in visual working memory. The first originates from Luck and Vogel's (1997) highly influential study, published in *Nature* and cited more than 900 times, which compared performance in conditions in which participants had to maintain only a single visual feature of each item in working memory (orientation *or* colour) to a conjunction condition in which they were required to maintain both visual features (orientation *and* colour). The rationale is that equivalent performance between conjunction and single visual feature conditions signifies that visual working memory automatically stores integrated representations. Luck and Vogel reported equivalent performance between these two conditions and suggested that this was evidence for an object based representational format. They do, however, concede that this pattern of results is also amenable to a representational format consisting of independent visual feature stores. This finding shows that participants automatically encode all visual feature values associated with an item, but says nothing about whether these visual features are maintained together in an integrated representation or whether they are stored in separate visual feature stores. Other authors have, however, mistakenly taken it as evidence for an integrated representation account of visual working memory maintenance (Ko & Seiffert, 2009; Landman et al., 2003). Luck and Vogel's integrated representation account then rests

on the results for their *colour-colour conjunction* experiment. In this task, participants were required to maintain information about items defined by more than one feature value along the *same* feature dimension (in this case, colour) and performance in this condition was the same as in conditions in which items were defined by a single colour (see [Figure 1.1](#) of the introduction). A number of studies have, however, failed to replicate this key finding (Delvenne & Bruyer, 2004; Olson & Jiang, 2002; Wheeler & Treisman, 2002), showing visual working memory capacity for items composed of a single colour to be greater than memory for bi-coloured items.

Wheeler and Treisman (2002) employed a more direct method of using change-detection tasks to assess visual working memory representational format, in which subjects were required to detect changes involving the addition of novel visual feature values (novel changes), as well as changes which involved the swapping of visual features between items (binding changes). Importantly, in the “2-feature” conditions, novel changes could occur within one of two feature dimensions (e.g. shape or colour), requiring participants to maintain information about the visual feature values of both dimensions. Binding conditions, on the other hand, required maintenance not only of all the visual feature values in a display, but also of the associations between the feature values of each dimension. The authors reasoned that if visual working memory maintains integrated wholes, there should be similar levels of performance for the two types of change. Contrary to this proposal, they found performance in detecting binding changes to be worse than novel change detection. This *binding deficit* suggests that the representational format of working memory consists of independent visual feature stores.

A striking feature of Wheeler and Treisman’s (2002) findings was the important role the nature of the test display had on the presence or absence of a binding deficit. Namely, the binding deficit completely disappeared if participants were presented with a single-item

display at test (Experiment 4B). The authors hypothesised that the cause of this disparity in results when presenting either one or many items at test was attentional. They proposed that attention is required to maintain binding information in visual working memory and that since processing the multiple items in a whole display also requires attentional resources, binding information is lost in working memory due to this reallocation of attention from working memory to perceptual processing. In contrast, a single test item draws on minimal resources, so the resources maintaining feature binding in working memory remain unaffected. Importantly, Wheeler and Treisman (2002) do not suggest that item information is unbound in visual working memory; rather, they propose a format which consists of independent channels specialised for the maintenance of single feature dimensions, with associative links maintaining binding information between visual feature channels. That is, they are *bound in a soft sense*. One of the key features of this proposal is that the basic building blocks of visual working memory representations are visual features, with the maintenance of binding information requiring additional resources. This stands in opposition to a conceptualisation of visual working memory that can be described as being *bound in a hard sense*, in which information is stored in a limited number of slots in visual working memory, with each slot filled by an integrated representation i.e. a single representation containing all of the visual features of the remembered item (Luck & Vogel, 1997; W. Zhang & Luck, 2008). Importantly, because this model of visual working memory regards the units of visual working memory to be the object, it regards the storage of binding information as being automatic and mandatory.

Wheeler and Treisman's (2002) hypothesis is enticing, but has not gone unchallenged. Johnson, Hollingworth and Luck (2008) have recently cast doubt on the very existence of a binding deficit in visual working memory, as well as on whether attention plays a primary role in maintaining binding information in visual working memory. The former criticism

relies on the fact that, while Wheeler and Treisman (2002) report a main effect of condition in their experiment 4A, no pairwise comparisons were reported, making their findings difficult to interpret. In this experiment, the three critical conditions were a binding condition, a novel colour condition and a novel shape condition, with the last two occurring in the same block, requiring participants to maintain both colour and shape information on any given trial. Although the binding condition produced the worst performance, it is unclear whether this was significantly worse than *both* novel feature conditions, or just the novel colour condition (the condition yielding highest performance).

This is indeed a valid criticism, because if the main effect of condition is driven solely by a high sensitivity to novel colour changes, this would seriously undermine the notion of separate visual feature stores in visual working memory. Instead, a more parsimonious account of Wheeler and Treisman's (2002) results would involve ascertaining the reasons for participants' increased sensitivity to colour changes in tasks involving multi-item test displays. One hypothesis of this nature, suggested by Johnson et al. (2008), is that the global, statistical colour properties of a display can be maintained in visual working memory, and it is changes to these global properties that are detected in novel colour changes — see Francis and Irwin (1998) for evidence of global colour properties being maintained in visual working memory. To determine whether it was simply an increased sensitivity to novel colour changes driving the binding deficit, Johnson et al. (2008) repeated the critical experiment reported by Wheeler and Treisman (2002) but ran a series of pairwise comparisons to assess whether there was any evidence for a binding deficit. This analysis showed that binding changes differed significantly only from novel colour changes and not from novel shape changes.

One potential concern with both the experiment of Wheeler and Treisman (2002) study that investigated shape-colour binding — as well as the subsequent methodological replication by Johnson et al. (2008) — is the role location may have played in assisting

performance in the binding condition. Both studies attempted to nullify the role of location by randomly placing the test display items in the locations occupied in the initial display, with the restriction that none of the shapes was in the same location for both initial and test displays. The problem with this is that colour-location binding can still be used to determine whether a change has occurred in certain situations. This is most easily described for cases in which set size is two: when there is no change in shape-colour binding, both colour-location and shape-location bindings change as the two items swap positions between initial and test displays; when there is a change, however, colour-location bindings, by logical necessity, stay the same between the initial and test displays. In other words, participants could employ a strategy whereby they determine a colour-shape binding change has occurred if any colours stay in the same location between the initial and test displays. This is illustrated visually in [Figure 2.1](#), using a set size of 3 as an example. While this issue becomes less of a concern as set size increases, the strategy can nonetheless still be employed successfully on a substantial proportion of trials<sup>9</sup>. This is especially true since Treisman and Zhang (2006) have shown that location plays an important role in retrieving binding information when the ISI between initial and test displays is 900ms (the ISI used in these studies). In the current study, I assessed visual feature binding in visual working memory using a change-detection task, but employed the crucial step of ensuring that location was completely non-informative. This was achieved by presenting the test display items in entirely novel locations.

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<sup>9</sup> For set sizes 4 and 6, it is possible that this strategy was prevented by ensuring that no colours and no shapes appeared at the same location for *change* trials. There is no mention of this in the methods section of either Wheeler and Treisman (2002) or Johnson et al. (2008)

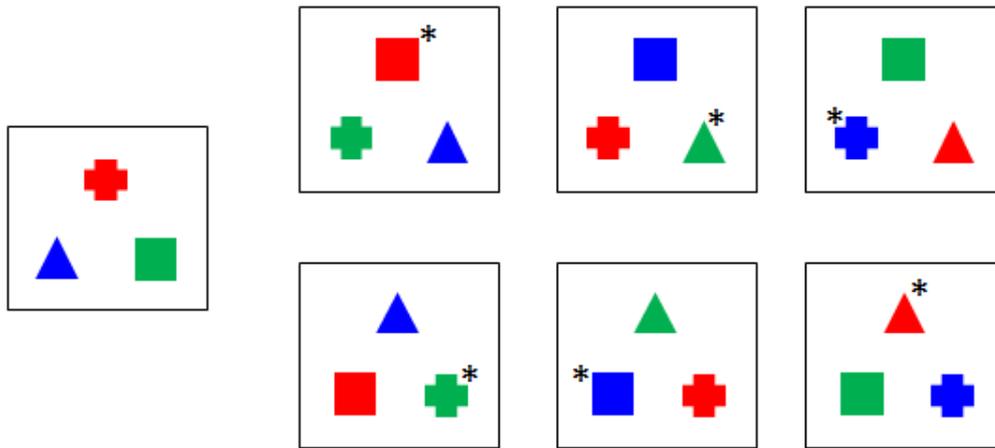


Figure 2.1. The left-most display depicts a hypothetical memory display of three items. For a set-size of three, there are only 2 permutations that ensure the test display does not involve a shape appearing in the same location as the initial display. These two permutations are depicted on the top and bottom rows. In addition, there are three combinations of shape-colour swaps. The left test display column shows displays in which the square and cross swap colours; the middle row shows occasions when the square and triangle swap colour; the right row shows a colour swap between the cross and the triangle. As can be seen in this figure, in each case there is always a colour that appears in the same location in the test display as it appeared in the initial display. These are denoted with an asterisk.

A secondary aim of the current study was to determine the effect of retroactive cues on performance in novel and binding conditions. Namely, we were interested in whether cueing an item in visual working memory with a single visual feature cue enables access to all of the visual features associated with an item. This is an important manipulation because it addresses directly the question of whether working memory representations are bound prior to presentation of the test display. While change-detection tasks have been used extensively to investigate aspects of visual working memory maintenance, such as capacity and representational format, it is clear that the nature of the test display — whether it is composed of one or many items — has a profound impact on the pattern of results. Thus, it is difficult to determine whether a particular set of results is due to working memory storage itself or to the subsequent effects of processing the test display.

One possibility is that the extra decision processes required to detect a change for multi-item test displays specifically disrupts binding in visual working memory. This was

discounted by Wheeler and Treisman (2002), because cueing a single item in the test display (i.e. reducing the number of comparisons to be made between working memory representations and items on the screen) did not improve performance in detecting binding changes relative to an uncued version of the task (experiment 5). Wheeler and Treisman (2002) interpreted this finding as evidence that the effect of whole displays on the maintenance of binding information can be attributed to the substantial “perceptual distraction” associated with perception of the test display.

What is the extent of visual feature binding prior to the presentation of a whole test display? Given that test displays composed of a single item produce equal performance for binding and novel changes (Wheeler & Treisman, 2002), parsimony suggests that feature and binding information are stored in equal degrees prior to any potential disruption from subsequent visual processing. As Allen, Baddeley and Hitch (2006) note, however, this result should be treated with caution as participants are able to employ a strategy in binding — but not novel — conditions that requires only partial retention of information from the initial display. More precisely, for any give set size ( $N$ ) participants need only maintain  $N-1$  items to detect all potential binding changes, while to detect all potential novel changes participants have to maintain all items in the original display. The simplest case, where  $N=2$ , illustrates this point: if an initial display contains a red X and a green T, participants can detect all binding changes by maintaining just the red X in working memory, as this information enables them to correctly regard both a green X and a red T as a change. The same is true if they maintain only the green T. Maintaining a single item in novel conditions, however, only allows detecting changes to the maintained item. When Allen et al. (2006) prevented this strategy by presenting, on a portion of catch-trials, a visual feature value twice in the test display (e.g. two red shapes or two squares of different colour) performance in the binding conditions dropped below both novel shape and novel colour conditions, suggesting that

visual feature information is maintained more readily in working memory than binding information. One drawback of this experiment, however, was the fact that colour, shape and binding conditions were all presented in separate blocks, meaning there was a difference in encoding demands between shape and colour conditions on one hand, and the binding condition on the other. That is, participants were required to encode less visual detail in the visual feature blocks (either shape or colour) compared to the binding condition (both shape and colour).

Another paradigm that could be used to investigate the degree of binding in visual working memory prior to the interference produced by a whole display involves the use of retro-cues presented between the initial and test displays. Retro-cues serve the function of informing the participant which item in memory could potentially change in the test display. A wealth of evidence from behavioural (Griffin & Nobre, 2003), ERP (Dell'Acqua, Sessa, Toffanin, Luria, & Jolicoeur, 2010; Griffin & Nobre, 2003) and neuroimaging (Nobre et al., 2004) studies has shown considerable functional and neural similarities between orienting attention to working memory representations and orienting attention to objects/locations in the external environment. This is usually achieved by presenting, in the delay period of a change-detection task, either a central cue pointing to the location of one of the just presented items (Delvenne, Cleeremans, & Laloyaux, 2010; Griffin & Nobre, 2003; Landman, Spekreijse, & Lamme, 2003; Lepsien, Griffin, Devlin, & Nobre, 2005; Makovski & Jiang, 2007; Makovski, Sussman, & Jiang, 2008; Matsukura, Luck, & Vecera, 2007; Nobre, Coull, et al., 2004) or a peripheral cue presented at the same location as an item from the initial display (Kuo, Yeh, Chen, & D'Esposito, 2011; Makovski & Jiang, 2007; Yeh, Yang, & Chiu, 2005).

Retro-cues have most commonly been used in experiments primarily concerned with visual working memory capacity, which have shown that performance in change-detection

tasks is substantially improved if informative cues are presented prior to the test display, suggesting that change-detection tasks underestimate the true capacity of visual working memory (Landman, Spekreijse, & Lamme, 2003; Makovski, Sussman, & Jiang, 2008; Sligte, Scholte, & Lamme, 2008). Retro-cues are also able to clarify the effect of multi-item test displays on binding in visual working memory, as these cues provide a measure of the extent of binding prior to the test display. That is, they can determine whether cueing an item in working memory during the delay period of a change-detection task enables access to all of the visual features associated with that item. The rationale is, in many ways, analogous to the partial report manipulation in iconic memory studies first reported by Sperling (1960); in the same way that partial reports of a briefly presented array allow access to the iconic memory trace before it decays, retro-cues in change-detection tasks provide an index of the extent of visual feature binding in working memory before it is disrupted by the whole display. By comparing performance in conditions where an item is cued with conditions where no item is cued in working memory, one can infer the level of binding during the delay period (from performance in the retro-cue conditions) and the extent to which it is disrupted by the test display (from performance in the no retro-cue conditions).

While spatial cues are universally used as retro-cues, a novel feature of the current study is that I investigated whether the enhancement of performance is also present when visual feature cues are used (i.e. colour or shape cues). As Makovski and Jiang (2007) note, it is not clear whether retro-cues result in attentional selection of locations, objects or visual features. This is particularly important for the issue of binding in working memory, as location seems to play an initial, facilitatory role in linking visual features in working memory – a role that becomes less important as duration of working memory maintenance increases (Jaswal & Logie, 2011; Treisman & Zhang, 2006). If this is the case, location cues could provide more direct access to binding information than visual feature cues.

To summarise, the current study had two objectives. First, the principal aim of the experiment was to determine whether a change-detection binding deficit, in which both novel visual feature conditions produce greater performance than the binding condition, occurs if location is made entirely uninformative by presenting initial and test display items in two separate sets of locations. This manipulation ensures that feature-location binding can never be used to aid performance, as in the case of previous research using this paradigm (Johnson et al., 2008; Wheeler & Treisman, 2002). Second, retro-cues were presented during the delay period to probe the degree of access to binding information prior to the onset of the test display. This has previously been assessed using a single item as a test display (Allen et al., 2006; Delvenne et al., 2010; Wheeler & Treisman, 2002), but this suffers from a confounding strategy in which participants need not maintain all items in the initial display to detect all changes in the binding condition (Allen et al. 2006). According to strong object-based theories of visual working memory, binding changes should not produce significantly poorer performance than both novel conditions regardless of whether an item is cued in visual working memory. Feature-based theories, on the other hand, propose that this pattern of results should only occur when an informative retro-cue is presented, as these cues should allow for protection of binding information against any subsequent interference from the test display. When no item is cued, however, feature-based theories predict that binding information will be preferentially lost from working memory, resulting in the reduced ability to detect binding changes relative to both novel change conditions.

## **2.2. Method**

### **2.2.1. Participants**

18 participants (9 males, 16 right handed) between the ages of 19 and 32 volunteered and participated in the study. Monetary compensation was provided for their time.

### **2.2.2. Stimuli**

All stimuli were presented on a light grey background using Presentation software. Seven letters (D, F, G, J, K, P and Y) and seven colours chosen to maximise discriminability (red, blue, green, yellow, violet, brown and black) were used to create the memory stimuli. Initial and test displays consisted of four letters. The locations of letters were randomised from trial to trial, with the constraint that they were positioned every  $90^\circ$  around an imaginary circle with a diameter subtending a visual angle of  $6.1^\circ$ . Each letter subtended a visual angle of approximately  $0.95^\circ$  from a viewing distance of approximately 57cm from the monitor. The four stimuli in the test display were then randomly allocated to the four locations  $45^\circ$  away from locations used in the test display.

There were 4 types of retro-cue: colour retro-cues consisted of a coloured circle presented in the centre of the screen that corresponded to a colour of one of the letters presented in the initial display; letter retro-cues consisted of white uppercase letters presented in the middle of the screen that corresponded to one of the letters presented in the test display; location cues consisted of a black outlined square centred on the location of one of the previously presented items; neutral cues, which consisted of a black outlined square in the middle of the screen. All retro-cue stimuli were the approximately the same size as the letter stimuli described earlier. The neutral cues functioned as a control condition because, while they provide visual stimulation to the participant in the delay condition (like the informative cues), they provide no information about which item is likely to change — see Griffin and Nobre (2003) and Matsukura, Luck and Vecera (2007) as examples of studies using neutral cues as a control condition as opposed to no cue at all.

### **2.2.3. Procedure and Design**

The experiment consisted of 3 blocks of trials each containing 144 trials. Each block contained an equal number of *change* and *no change* trials. All change trials involved changes to two items; by definition, binding changes involve changes to two items, so to maintain parity between novel and binding conditions two items also change in the novel conditions. Two blocks involved *novel* changes, in which change trials involved either novel colour changes (25% of trials) or novel letter changes (25% of trials). The other block contained binding changes, which involved two letters swapping colours. There were twice as many novel blocks as there were blocks with binding changes so that each type of change consisted of the same number of *change* trials. Block order was counterbalanced using an AAB, ABA, BAA design so as to distribute practice and fatigue effects equally across the three types of change. Each block contained an equal number of the four types of cue. 16 practice trials were presented prior to the first novel block and the binding block.

Each trial consisted of the following sequence of events (see [Figure 2.2](#) for a graphical depiction). A two digit number was presented which the participant was instructed to repeat rhythmically for the sequence of the trial. Given that the stimuli were letters, this phase is particularly important in the current study, as articulatory suppression reliably prevents verbal coding of visual information in working memory (Vogel, Woodman, & Luck, 2001). This was emphasised to participants, and care was taken to ensure they performed this phase to satisfaction during the practice blocks. Audio recordings were made to check that articulatory suppression performance was maintained throughout the experiment. Following a fixation cross, the initial display was presented and stayed on the screen for 1000ms. After a 900ms delay, one of four cues were presented for 100ms, three of which were informative. If an informative cue was presented, participants were instructed to continue to remember only the

relevant item in visual working memory, and that if there was a change between the initial and test displays it would always involve the cued item. After a second delay period (of 1000ms), the test display was presented. Half of the participants pressed “1” on the number keypad for “no-change” responses, and “2” for “change” responses. The responses were reversed for the other half of participants. Participants were instructed to make speeded responses, but informed that accuracy was of prime importance. Accuracy feedback was given at the end of each trial, by presenting the words “Wrong” or “Correct” on the monitor after each response. Each trial was self-initiated by the subject with a press of the spacebar.

### **2.3. Results and Discussion**

Results were analysed using a 3 x 3 repeated measures ANOVA with the following factors: *type of change* (binding, novel colour, novel letter) and *cue* (neutral, location, and feature). For binding trials, the feature cue results were averaged across colour and letter cues; for novel letter trials, the feature cue was a colour cue; for novel colour change trials, the visual feature cue was a letter cue<sup>10</sup>.

#### **2.3.1. Change-detection performance**

The measure of change-detection performance reported here is  $d'$ .  $d'$  values were transformed for all participants using the loglinear method to account for hit rates of 1 and

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<sup>10</sup> Trials in which a letter cue was paired with a novel letter change or a colour cue was paired a novel colour change were not included in this analysis as correct responses in these trials can be made independently of working memory storage. For example, if the cue is a red circle and there is no red item in the test display, it is simple to determine that there has been a colour change and respond accordingly. While these trials were not included in the analysis, they play an important role in the experiment as they ensured that participants were not able to deduce the type of change based on the cue in the novel change blocks.

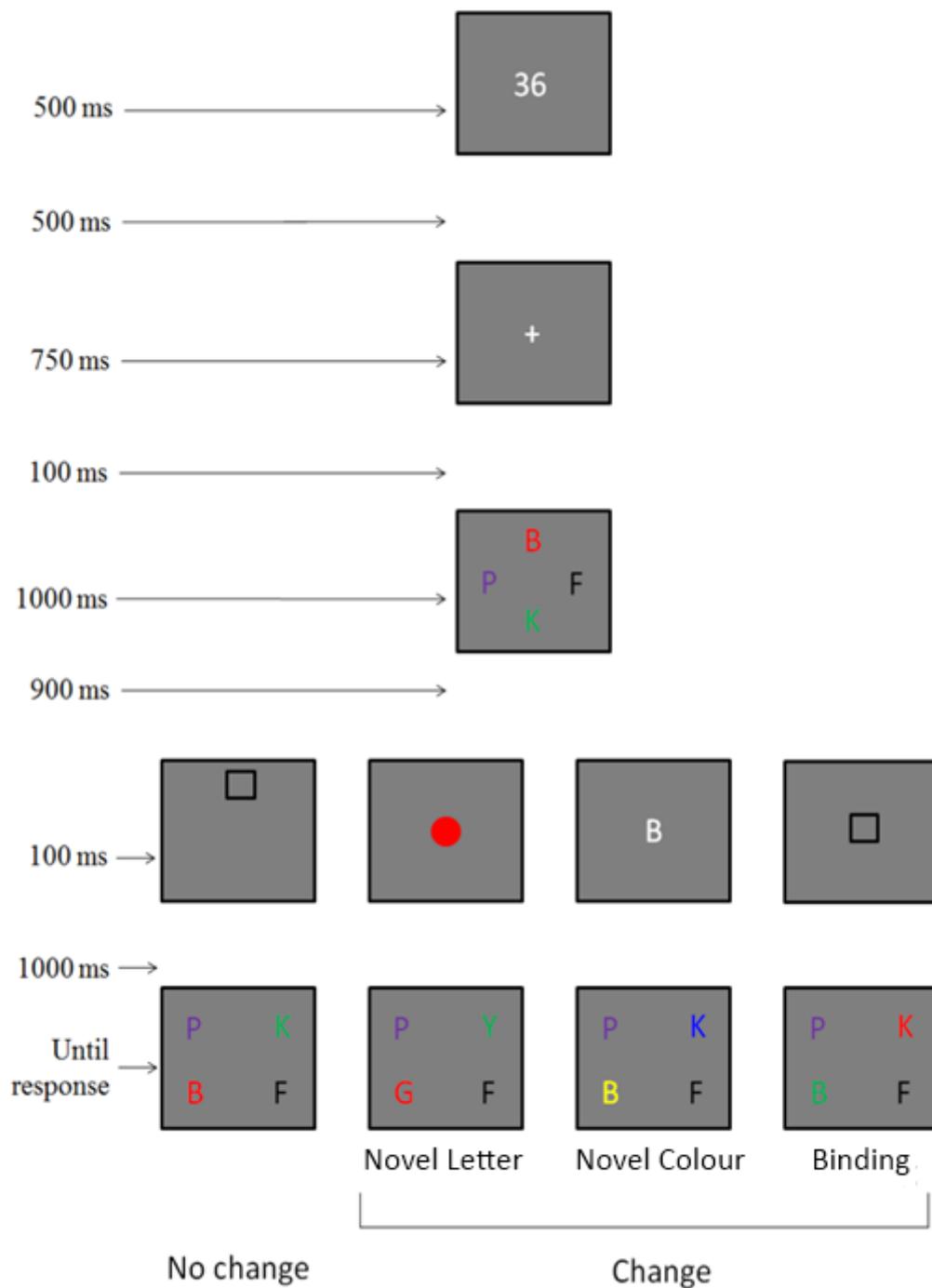


Figure 2.2. Schematic of the sequence of events in Study 1. 900ms after the offset of the initial display, one of four cue-types (location, colour, letter or neutral) was presented, after which a test display was presented which was either the same as or different to the initial display. These four cues were presented in equivalent proportions for all experimental blocks. “Change” trials consisted of novel letter, novel colour or binding changes. Novel letter and novel colour changes were presented in the same blocks, while binding changes were presented in a separate block.

false alarm rates of 0 (Hautus, 1995). The measures of corrected recognition and  $A_z$  were also calculated for all experiments reported here producing highly similar results.

A repeated measures ANOVA produced a main effect for *cue* with neutral cues ( $d' = 1.12$ ) producing significantly worse performance than both location ( $d' = 1.82$ ) and feature ( $d' = 1.72$ ) cues,  $F(2, 34) = 20.28$ ,  $p < .0001$ , partial  $\eta^2 = 0.544$ . There was a main effect of *type of change*,  $F(2, 34) = 22.22$ ,  $p < .0001$ , partial  $\eta^2 = 0.567$ , with performance in the novel colour ( $d' = 1.93$ ) exceeding novel letter ( $d' = 1.49$ ) and binding ( $d' = 1.23$ ) performance. Importantly, pairwise comparisons (Bonferroni corrected) showed binding performance to be worse than *both* colour ( $p < .001$ ) and letter ( $p < .05$ ) performance. The significant *cue x type of change* interaction ( $F(2.31, 39.21) = 3.47^*$ ,  $p < 0.05$ , partial  $\eta^2 = 0.170$ <sup>11</sup>) suggested, however, that this effect may not be apparent for all cue types. Because I was interested in the presence or absence of a binding deficit, as defined by Johnson et al. (2008), we unpacked this interaction by performing Bonferroni-corrected pairwise comparisons between the three types of change for each cue type. A binding deficit, in which performance in the binding condition was significantly worse than both novel and colour conditions was only apparent when neutral cues were presented — see [Figure 2.3](#).

Observation of the hit and correct rejection rates, shown in [Table 2.1](#), shows that while accuracy in the *no-change* trials were generally similar across the experiment (ranging from .75-.83), it was differences in performance in the change trials that seem to be driving the effects observed in the analysis of  $d'$  values. Indeed, a repeated measures ANOVA on proportion correct values on only the *no-change* trials (i.e. correct rejection rates) showed no significant effects of *cue* ( $p = .406$ ), *type of change* ( $p = .070$ ) or the interaction between these two factors ( $p = .099$ ). When the same analysis was performed on the *change* trials (i.e.

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<sup>11</sup> Results with asterisks next to them have been corrected using Greenhouse-Geisser corrections.

hit rates), the same pattern of results emerged as was the case for the  $d'$  analysis. That is, there were significant effects of *cue* ( $F(1.52, 25.81) = 49.45^*$ ,  $p < .001$ ), *type of change* ( $F(2, 34) = 20.62$ ,  $p < .001$ ) and a significant interaction ( $F(2.56, 43.52) = 9.54$ ,  $p < .001$ ).

Table 2.1. Proportion correct for change and no-change trials (i.e. hit rates/correct rejection rates) for all *cue* x *type of change* combinations

	Colour	Letter	Binding
Neutral	.76/.81	.56/.81	.40/.79
Location	.89/.83	.79/.83	.77/.75
Feature	.87/.75	.73/.81	.78/.77

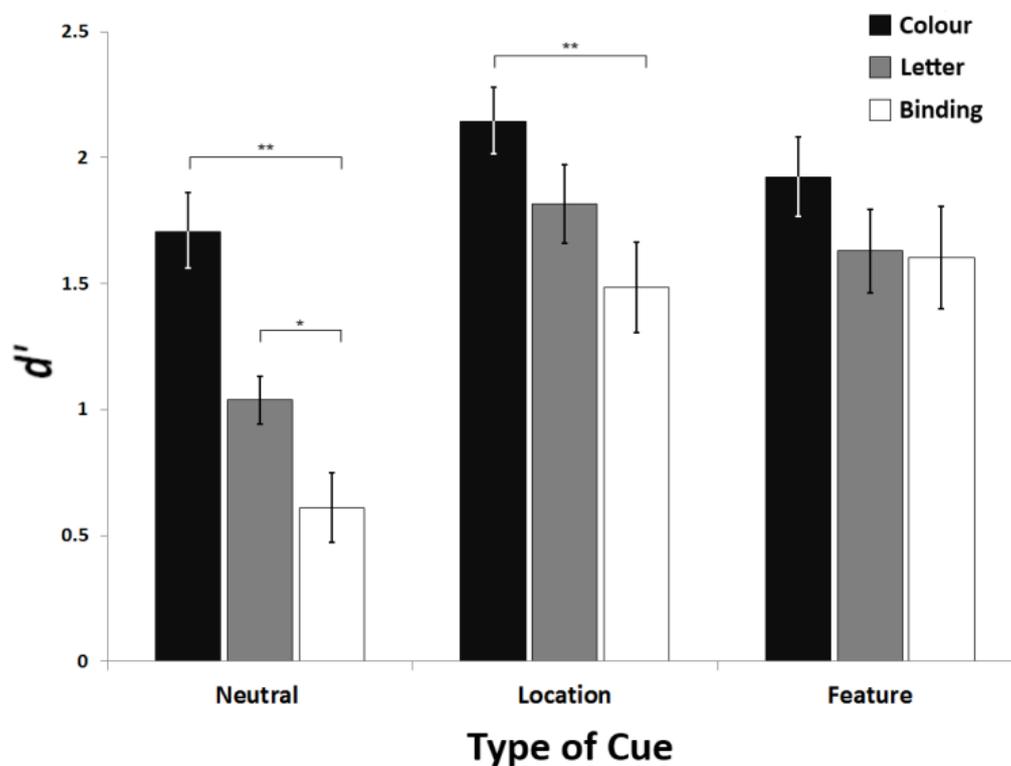


Figure 2.3. Mean  $d'$  scores and standard errors for the three types of change across the different types of cue in Experiment 1. Pairwise comparisons producing a Bonferroni corrected p-value  $< .005$  are denoted by \*\*, while p-values  $< .05$  are denoted by \*.

### **2.3.2. Response times**

The following are from correct *change* trials only i.e. the time taken to successfully detect a change — see Figure 2.4. A repeated measures ANOVA showed a significant main effect of *type of change*, with responses to novel colour changes ( $M = 902\text{ms}$ ) being consistently

faster than novel letter ( $M = 977\text{ms}$ ) and binding ( $M = 1027\text{ms}$ ) changes,  $F(1.19, 20.24) = 5.53^*$ ,  $p < 0.05$ , partial  $\eta^2 = 0.246$ . A main effect of *type of cue* was also present,  $F(2,34) = 22.76$ ,  $p < 0.001$ , partial  $\eta^2 = 0.572$ . This effect is driven by responses to neutral cue trials being significantly slower than trials involving informative cues. There was no significant interaction between type of cue and type of change ( $p = .15$ ).

The relative effect of retro-cues on change-detection performance for binding and novel changes has previously been investigated by Yeh, Yang and Chiu (2005), who reported no interaction between type of change and cue type. That is, performance was superior in the novel colour condition (compared to their binding condition) regardless of the presence or absence of a spatial retro-cue. It is difficult to extrapolate their findings to feature binding, however, as the relevant experiments only used a single feature dimension (colour) and, as such, was investigating only colour-location binding.

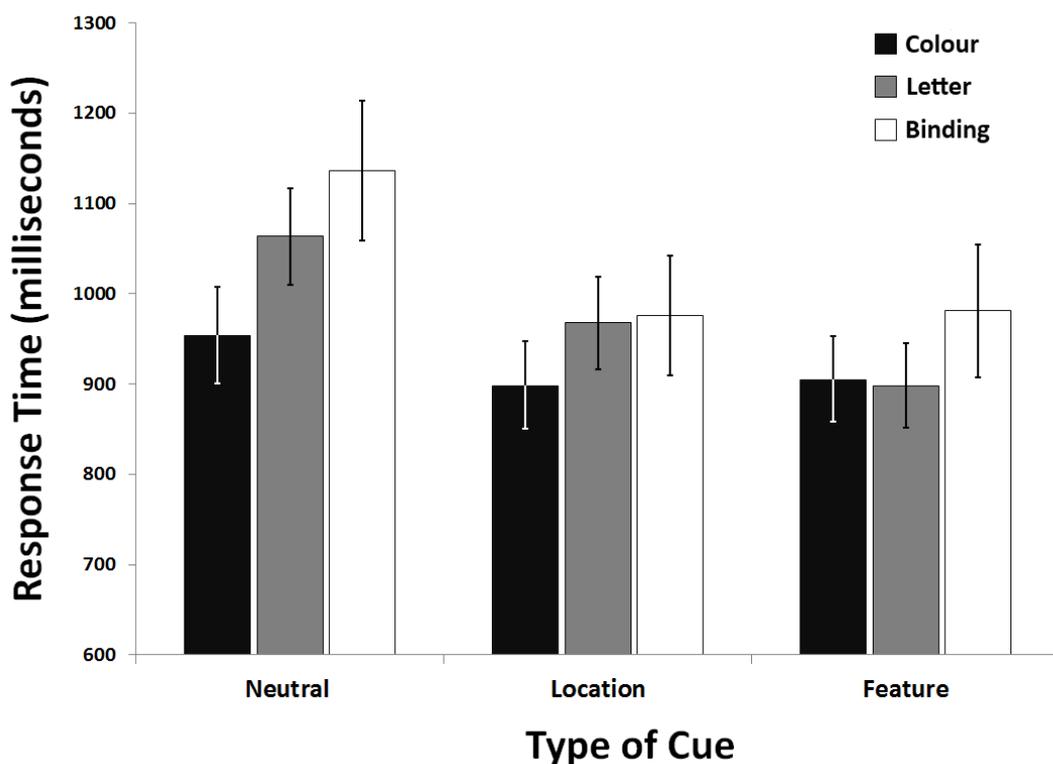


Figure 2.4. Mean response times and standard errors observed in *change* trials for the three types of change across the different types of cue.

Similarly, the results of experiment 1 may seem to contradict recent findings in which performance in novel and binding conditions were equally enhanced by the presentation of an informative retro-cue in the delay period of a change-detection task (Delvenne et al., 2010) , while the current study showed informative retro-cues to have a differential effect on novel and binding changes. The differences in the findings of the two studies are not that surprising, however, as they used slightly different methodologies and were motivated by different questions. Delvenne et al. (2010) cued two items in working memory and presented a single item as the test display in their change-detection tasks. Two items were cued because, as the authors rightly point out, maintenance of binding information can only be tested when more than one object is maintained in working memory. That is, cueing two items results in maintaining not just two colours and two shapes, but the associations between the pairs of colours and shapes. This was necessary for Delvenne and colleagues' experiment, as they were interested in the maintenance of binding information after the cue was presented<sup>12</sup>. Experiment 1 of the current study cued a single item because we were interested not in the maintenance of binding information *after* the cue, but the degree to which the cue provided access to all the visual features associated with the cued item. That is, the current study was interested in the extent of feature binding prior to any interference produced by the test display.

To summarise, experiment 1 showed that detection of binding changes is more difficult than novel changes when location is made entirely uninformative and no informative cue is

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<sup>12</sup> It should be noted, however, that cueing two items and using a single probe as a test display is an inappropriate way of comparing maintenance of feature and binding information because, as mentioned earlier and noted by Allen et al. (2006), participants need only maintain one of the two items to detect all binding changes. Detecting all novel changes requires maintaining both pairs of shapes and colours.

presented prior to the test display. This finding is best explained by a model of visual working memory in which binding information is either less likely to be maintained in working memory (relative to visual feature information) or is preferentially lost upon presentation of the test display (Fougnie & Marois, 2009; Wheeler & Treisman, 2002). The fact that binding information is largely accessible prior to the onset of the test display, as seen by the increased performance due to an informative retro-cue, is supportive of the latter of these two possibilities. Alternative hypotheses, which propose that binding information is automatic and does not incur additional costs (Luck & Vogel, 1997), are unable to explain the fact that binding information is particularly susceptible to interference from the test display when an item in visual working memory is not cued.

## **2.4. General Discussion**

The apparent simplicity of change-detection tasks has made them the most commonly used paradigm for investigations of both visual working memory capacity and the representational format of information maintained in visual working memory. While the paradigm has been used to support both integrated object models of visual working memory (Luck & Vogel, 1997; Vogel et al., 2001) and feature channel models (Delvenne & Bruyer, 2004; Treisman & Zhang, 2006; Wheeler & Treisman, 2002), it has become clear that performance in these tasks depends as much on the extent of perceptual interference associated with the test display as on the nature of visual working memory representations. This is illustrated by the discrepancy in results between change-detection tasks involving multi or single item test displays (Wheeler & Treisman, 2002).

Experiment 1 assessed the extent to which a whole test display disrupts binding in visual working memory when none of the stored items is cued relative to when a single item is cued. Presentation of an informative retro-cue prior to the onset of a test display, whether it was a

feature cue (colour or letter) or a location cue, resulted in increased performance relative to neutral (uninformative) cues. Furthermore, this increase in performance was most pronounced for binding changes; while a neutral cue resulted in a binding deficit (i.e. binding change-detection performance being significantly poorer than both novel feature changes), this was not the case when an informative cue was presented in the test display. In other words, memory for binding information was disrupted by processing of the test display more than memory for individual visual features<sup>13</sup>. This analysis was performed with specific reference to concerns raised by Johnson et al. (2008) regarding the criterion for determining whether visual working memory capacity for visual features is greater than for binding information. Showing that capacity for both colour and letter information is greater than memory for binding information precludes interpreting the binding deficit as resulting solely from something particular to working memory for colour information e.g. the encoding and maintenance of the global statistical colour properties of the initial display. Johnson and colleagues (2008) presented findings (Exp. 3) showing that, when participants were required to maintain both colour and shape information (the “2-feature” condition), only the detection of novel colours (but not novel shapes) was greater than performance in a binding condition. The results of experiment 1 of the current study partially support this proposal, as detecting novel colours is the easiest change to detect, generally showing the highest accuracy and lowest response times. Importantly, however, accuracy in detecting novel letter changes was also greater than detection of binding changes for the neutral cues. There are a number of possible reasons for this discrepancy.

First, our study used letters and capacity for letters has been shown to be greater than other stimulus types, including line drawings of objects and shapes (Alvarez & Cavanagh, 2004;

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<sup>13</sup> A similar interpretation is that informative cues protect binding information from any subsequent disruption by the test display.

Treisman & Zhang, 2006). It is likely that capacity for letters also exceeds capacity for the shapes used by Johnson et al. (2008), although an interesting question requiring further investigation is whether performance in detecting different types of identity-colour binding changes also vary by stimulus type. For example, if capacity for letters is greater than random polygon shapes, is it also the case that memory for letter-colour bindings is greater than polygon-colour bindings? Another possible reason for the difference in findings could be the presence of the neutral cue in our study, which could potentially disrupt binding in visual working memory. This is unlikely to be true, however, as recent work by Ueno, Allen, Baddeley, Hitch and Saito (2011) has shown that a visual suffix, passively viewed in the delay period of a change-detection task, does not differentially disrupt binding in visual working memory relative to visual features if the suffix could not plausibly be an item from the initial display. Instead, the most likely reason for the discrepancy is that our design used novel locations (not used in the initial display) for test display items. This prevents employment of strategies, available to participants when test display items are randomised within the same locations used in the initial display, which take advantage of feature-location binding information (see the introduction for a more detailed description of these strategies).

While the results of the neutral cue conditions show that binding information is preferentially lost from working memory, the nature of this memory failure is not clear. It could be the case that binding information undergoes decay more rapidly than visual feature information. While binding information may still be present in working memory when the informative cues were presented (900ms after the offset of the initial display), as shown by the increased performance in the binding condition, it may have undergone extensive decay by the time of the presentation of the test display in the neutral cue condition (2000ms after the offset of the initial display). This is unlikely to be the case, however, as recent findings have shown that binding information is available as readily 4000ms after an initial display as

it is at much shorter delay periods (Jaswal & Logie, 2011; Logie, Brockmole, & Jaswal, 2011). The more likely explanation attributes the loss of binding information to the interference produced by the perceptual processing of the test display. This explanation comes in a number of flavours. The first proposes that attention is required to maintain binding in visual working memory, and that processing the items in the test display causes a shifting of attention from working memory representations to perceptual processes, resulting in the loss of binding information from working memory (Wheeler & Treisman, 2002). The second hypothesis, proposed by Allen and colleagues (2006), proposes that the encoding and maintenance of binding information is an automatic process (i.e. it doesn't require any "extra" resources), but that binding information is more fragile and prone to interference than visual feature information. Closely related to this is the notion that binding fails because binding information is "over-written" by the new feature associations presented in the test display (Alvarez & Thompson, 2009). While beyond the scope of the current experiment, there are compelling reasons that the attentional account is unlikely to be true, as a number of studies have shown that a variety of attentionally demanding secondary tasks, presented during the delay period, do not preferentially disrupt binding information in working memory relative to visual feature information (Allen, Baddeley, & Hitch, 2006; Johnson, Hollingworth, & Luck, 2008; Stevanovski & Jolicœur, 2011; Yeh, Yang, & Chiu, 2005, but see Fougne & Marois, 2009)

In conclusion, the results reported here provide evidence against models that regard the unit of visual working memory to be the integrated object, stored in an all or none fashion. Instead, they support models of visual working memory that allow for differential processing of visual feature and binding information. This difference is captured by the varying degrees to which multi-item test displays disrupt working memory for binding and visual feature information when confounding strategies are controlled for. This is in agreement with recent

studies employing more sophisticated “mixture modelling” paradigms, which have shown visual features to be maintained independently in visual working memory (Bays et al., 2011; Fougne et al., 2010). Lastly, while the current set of data are generally supportive of a feature-channel account of working memory representation, it does not speak to the debate about whether binding fails in whole-display change-detection tasks because a) binding requires attention (Fougne & Marois, 2009; Wheeler & Treisman, 2002), or b) binding, while automatic and not dependent on attention, is especially sensitive to interference (Allen et al., 2006) or c) colour-shape associations are over-written by incoming visual information (Alvarez & Thompson, 2009).

## **Chapter 3: Study 2 – Evidence for feature-based representation in working memory using a novel two-alternative forced choice paradigm**

### **3.1. Introduction**

A central debate in visual working memory research concerns the nature of maintained representations. The object hypothesis proposes that representations are maintained as integrated wholes in a limited number of “slots” in visual working memory (Luck & Vogel, 1997; W. Zhang & Luck, 2008). The feature channel hypothesis posits that visual working memory consists of independent stores or channels, each maintaining different feature dimensions such as colour, form, orientation and so on, with additional links maintaining associations across feature channels (Allen et al., 2006; Bays et al., 2011; Brady et al., 2011; Corballis, Armstrong, & Zhu, 2007; Delvenne & Bruyer, 2004; Wheeler & Treisman, 2002). There are two forms of the feature channel hypothesis: one account regards the maintenance of binding information as requiring additional attentional resources (Wheeler & Treisman, 2002), while others propose that while the maintenance of binding information is automatic, binding information is particularly fragile and prone to interference (Allen et al., 2006) or over-writing (Alvarez & Thompson, 2009) from subsequent visual input. The chief distinction between object and feature channel hypotheses is that the former predicts the maintenance (and subsequent decay/interference) of object information to be all-or-none, while the feature-channel hypothesis allows for the possibility of certain visual features being maintained (or forgotten) more readily than others, even if they correspond to the same object. The feature-channel hypothesis also allows for the possibility of the associations between visual features to undergo decay or interference independently of the loss of the visual features themselves.

The most common paradigm for investigating this question is the change-detection paradigm, in which some measure of accuracy (e.g. proportion correct, corrected recognition,

$d'$ ,  $A'$ ) is used as the primary measure of performance. Despite this paradigm's popularity, it has produced a number of contradictory results. For example, Luck and Vogel (1997) provided supporting evidence for the object hypothesis by showing that accuracy drops sharply when set size is greater than four items, suggesting that visual working memory capacity is limited to 3-4 objects. In addition, this pattern of performance occurred regardless of the number of visual features present in each object. Importantly, this was also the case when these visual features were from the same dimension e.g. performance was similar when maintaining four objects made of eight colours compared to four objects made of four colours, suggesting that the basic unit of visual working memory storage is the integrated object. This result has, however, failed to be replicated with a number of research groups showing that maintaining bi-coloured objects is more difficult than objects defined by a single colour (Delvenne & Bruyer, 2004; Olson & Jiang, 2002; Wheeler & Treisman, 2002) .

Similarly, direct tests of the degree of binding in visual working memory have failed to produce consensus. Wheeler and Treisman (2002) compared performance in a binding condition (in which items swapped visual features between initial and test displays) and two novel feature conditions (in which either new shapes or colours were presented in the test display) finding a significant binding deficit effect, with the binding condition producing the least accurate performance. It is not clear, however, whether accuracy in the binding condition was lower than both novel shape and novel colour conditions. Johnson, Hollingworth, and Luck (2008) replicated Wheeler and Treisman's experimental design and found only the colour condition produced greater levels of accuracy than the binding condition. This discrepancy in findings extends to designs that involve a single item as the test display: Wheeler and Treisman (2002) showed no difference between binding changes and both novel colour and novel shape conditions for single item test displays; Delvenne, Cleeremans and Laloyaux (2010) found

accuracy in the binding condition to be worse than a novel colour condition but not a novel shape condition; Ueno, Allen, Baddeley, Hitch, and Saito (2011) have produced results from a series of single display change-detection experiments that consistently show worse performance for binding changes relative to both novel colour and novel shape conditions. While it is very difficult to ascertain precisely why these similar experiments produce such different results, it does suggest that measures of accuracy may be an unreliable measure to assess the nature of visual working memory representations.

Contradictory experimental results aside, a major concern with using accuracy as the primary measure of performance in single display change-detection tasks is the potential use of a confounding strategy by participants. This strategy, described by Allen, Baddeley and Hitch (2006) enables detection of a binding change to a given item even if that item is not maintained in working memory. For example, if an initial display contains a red X and a blue T, one need only maintain the red X to detect all possible binding changes<sup>14</sup>, while both items need to be maintained to detect all novel changes. When this strategy is controlled for, performance in binding conditions drops below both novel shape and novel colour conditions (Allen et al., 2006).

While the results from change-detection paradigms are inconclusive, evidence from two other sources provide support for feature channel hypotheses. First, a recent study has used mixture modelling methods (W. Zhang & Luck, 2008) to assess the nature of errors made by participants when they are required, on each trial, to recall two feature values (colour and orientation) associated with a probed item in working memory (Bays et al., 2011). Their results showed that when participants made random guesses, they often do so only along a single feature dimension. That is, on a significant proportion of trials, participants maintained

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<sup>14</sup> Both possible changes (red T and blue X) should be correctly judged as different as each item shares only a single visual feature value with the red X held in memory.

only the colour of an object and not its orientation (and vice versa). In addition, when participants make the error of reporting visual feature values associated with non-probed items, it is most often the case that these misreported visual feature values do *not* correspond to the same non-probed item. Both sets of results directly contradict models of working memory that posit fully integrated representations occupying a limited number of slots. Using a similar paradigm, Fougne and Alvarez (2011) have replicated the independence of colour and orientation maintenance in working memory, but showed that this independence did not extend to the visual features of width and height.

The second body of research providing supporting evidence for feature channel hypotheses comes from neuroimaging work that has highlighted the overlap in regions supporting both visual perception and visual working memory — for reviews see D’Esposito (2007; Pasternak & Greenlee (2005); Postle (2006); Slotnick (2004). As emphasised by Slotnick (2004), a critical property of neural overlap is that the feature-based modularity observed in posterior regions recruited by visual perception (Tootell et al., 1996) extends to visual working memory. That is, the maintenance of information in visual working memory involves the sustained activity of regions responsible for processing independent visual features. Neuroimaging evidence (Serences, Ester, Vogel, & Awh, 2009) supporting this sensory recruitment model has shown that voxels as early as V1 show specificity for orientation or colour in visual perception, and that this specificity carries over to working memory maintenance.

The current study employed a combination of two paradigms, neither of which has been applied to issue of binding in visual working memory. Instead of the same-different judgment required of change-detection tasks, I used a two-alternative forced choice task in which participants were presented with a test display containing two items and required to select the one that matched an item in visual working memory. Manipulating the nature of the lure

enables comparison of conditions in which the lure contains a novel visual feature (not present in the initial display) with a binding condition in which the lure is a recombination of visual features presented in the initial display (i.e. an object comprised of a shape and colour present in the initial display, but in a combination not present in the initial display). An additional benefit of the 2AFC paradigm is that it minimises response bias (Macmillan & Creelman, 2005). Previous work has shown performance in 2AFC tasks to be poorer than single-display change-detection tasks when the stimuli were simple colour patches (Makovski et al., 2010), but it is an open question whether a 2AFC task would produce a binding deficit .

I also required participants to select the item using the mouse, enabling continuous recording of mouse movements, thereby providing a set of measurements that reveal important information about the time-course of decision making in the 2AFC task. This paradigm regards the target and lure as being in competition for selection throughout the trial, and has been used fruitfully in the investigation of a number of domains e.g. racial and gender stereotyping (Freeman, Pauker, Apfelbaum, & Ambady, 2010; K. L. Johnson, Freeman, & Pauker, 2011), semantic categorisation (Dale, Kehoe, & Spivey, 2007), syntactic processing (Farmer, Cargill, & Spivey, 2007) as well as the more “lower-level” task of visual search (Song & Nakayama, 2008)<sup>15</sup>. It is based on the principle that evidence-accumulation — both perceptual and cognitive — continuously biases motor output throughout the trial, even before a final decision is made (Magnuson, 2005). While classical cognitive science regards perception, cognition and action as distinct sets of processes (e.g. Fodor, 1983; Pylyshyn, 1984), the notion that online recording of movement can provide an index of perception and cognition is supported by a large body of work showing that motor preparation and movement unfold in parallel with — and not subsequent to — perception and

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<sup>15</sup> This study recorded hand movements during pointing instead of the x,y coordinates of mouse movements. The principle of perception and cognition continually modulating movements is shared by both paradigms.

cognition. For example, the mere presentation of action sentences induces an increased BOLD response in motor circuits of the brain (Tettamanti et al., 2005). In addition, electrophysiological studies on monkeys have shown that neurons in the primary motor cortex represent not only behavioural output (i.e. motor movement execution), but are also sensitive to the relevant stimulus properties of sensory input (J. Zhang, Riehle, Requin, & Kornblum, 1997). Of particular importance to the current paradigm, Cisek and Kalaska (2005) have shown that when monkeys are faced with a decision requiring a reaching movement to one of two options, neurons in premotor cortex simultaneously generate distinct representations for both potential movements. It was only after presentation of a non-spatial cue did the signal associated with the cued movement increase in strength relative to the uncued movement. This finding is important as it clearly shows that movement preparation occurs in parallel with perceptual and cognitive processes. Fine-grained measurements (e.g. trajectory and complexity) of mouse movements made *during* the decision process provide a potentially rich source of data to accompany accuracy measures, which have shown to be an unreliable measure of performance in change-detection tasks.

Performance in a memory based 2AFC task involves a decision rule in which participants assess the memory strength of the target and lure independently, and select the item with the greatest memory strength (D. G. Smith & Duncan, 2004). If visual working memory maintains holistic representations, the memory strength of each item would be determined by independently comparing each item to integrated representations in working memory (“Does this item match an object in any working memory slot?”). It follows that the memory strength of the lure in a 2AFC task should be equivalent in visual feature and binding conditions; in both cases, the lure would not match an integrated representation in working memory. That is, in both cases, the lure is a novel object and should have an evidence distribution centred on zero. This account predicts no differences between binding and visual feature conditions

in terms of both accuracy and mouse movements. Alternatively, if visual working memory maintains information in the form of visual feature channels bound together by associative links, the memory strength of each item is determined by a number of independent comparisons based on visual features and their associations (“Does this item match a colour in working memory?”; “Does this item match a shape in working memory?”; “Does this item match a shape-colour combination in working memory?”). If this is the case, the memory strength of the lure would be different for visual feature and binding conditions: in the visual feature condition, only one visual feature in the lure would map onto information in visual working memory (low memory strength); in the binding condition *both* visual features present in the lure are also present in working memory (high memory strength). This increased memory strength of the lure in the binding condition could manifest itself in a number of ways. Easier discrimination of the target and the lure should result in higher accuracy for novel conditions relative to the binding condition. Furthermore, there should be differences in mouse movements for novel and binding conditions; the higher memory strength of the lure in the binding condition (relative to the visual feature conditions) should result in greater competition between target and lure, causing mouse movements that gravitate towards the target later than is the case for visual feature conditions.

## **3.2. Method**

### **3.2.1. Participants**

18 right handed participants (6 males) from the University of Auckland community volunteered to take part in the experiment. All participants used their right hand when making mouse movements.

### **3.2.2. Stimuli**

All stimuli were presented on a light grey background using Presentation software (www.neurobs.com). Six shapes (shown in [Figure 3.1](#)), chosen to minimize recoding of stimuli as verbal representations, were used as stimuli for the experiment. Each stimulus could occur in one of six colours chosen to maximize discriminability (white, black, red, blue, yellow and green), and each stimulus subtended an angle of approximately  $1^\circ$  when viewed from a distance of 57cm. The mouse cursor used was a small fixation cross.



Figure 3.1. The stimuli used in the experiment

### **3.2.3. Procedure**

Each trial began with a central fixation cross for 500ms. After an ISI of 500ms, the initial display of 3 items was presented for 1500ms in a triangular array around an imaginary circle subtending an angle of  $2.8^\circ$ . After a 2500ms delay, a warning tone was presented. This tone provided the signal for participants to slowly begin moving the mouse upwards, even though the mouse cursor was not yet present on the screen. This was done to ensure the cursor would be already moving upwards when the test array was presented<sup>16</sup>. 1000ms after the onset of the tone, the cursor appeared at the bottom of the screen (coordinates in pixels: 0, -300), together with the target and lure in the top left and right quadrants of the monitor. The top left item

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<sup>16</sup> This is important as it reduces the likelihood of participants holding the mouse in a stationary position while they make decisions, followed by a straight-line trajectory to their selection. If participants were to do this, mouse trajectories would not provide any information about the decision making process itself (besides a measure of the time taken to come to a decision, as indexed by the time taken to initiate movement). Ensuring that participants are moving the mouse *during* the decision process allows insight into the decision process not captured by traditional time-based measures of performance (e.g. response time).

was at coordinates -250, 300, while the top right item was at 250,300. The target was defined as the item having the precise shape-colour combination as one of the items in the original memory set. Both the target and lure were surrounded by a white square, subtending  $1.6^\circ$ . The target was presented on the left and right equally often. The trial ended when the participant moved the cursor into one of the white squares surrounding the target and lure and made a single click on the left mouse button.

There were four types of lure (shown in [Figure 3.2](#)), occurring equally often: i) the same shape as the target, but in the colour of one of the other two items from the initial display; ii) the same colour as the target, but one of the other two shapes from the initial display; iii) the same shape as the target, but a novel colour not present in the initial display; and iv) the same colour as the target, but a shape not present in the initial display. The first two constituted the binding condition, the latter two the novel colour and novel shape conditions. Note that the target and lure differ by a single visual-feature value for both binding and novel conditions.

There were 16 practice trials, during which the participants accustomed themselves to the task and especially to the movement of the mouse. If the participant or experimenter felt they were not proficient after 16 trials, another practice block was presented. Each participant was presented with 120 experimental trials. Accuracy feedback was provided after each trial with the words “Correct” or “Wrong” presented on the screen. After each trial participants were instructed to return the mouse to original position on the mouse pad and hit the spacebar key when they were ready to begin the next trial. A break was provided after 60 trials.

### **3.3. Results and Discussion**

### **3.3.1. Sensitivity performance**

$d'$  was calculated for each condition within each participant by using the conversion table specified by Hacker and Ratcliff (1979) to transform proportion correct values. The statistical results described below were almost identical when using proportion correct as a measure of accuracy performance. A repeated measures ANOVA with *condition* (binding/colour/shape) as the sole factor showed a significant effect,  $F(2,34) = 5.91$ ,  $p < .01$ , partial  $\eta^2 = .258$ . Given that I was primarily concerned with only the differences between binding and novel conditions, planned pairwise comparisons were run comparing each novel condition to the binding condition. This showed that while sensitivity in novel colour condition was significantly greater than the binding condition ( $p = .017$ ), this was not the case for the novel shape > binding comparison ( $p = .257$ ) — see [Figure 3.3](#).

### **3.3.2. Mouse trajectory data**

Only correct trials are included in the analysis of mouse movements. For each trial, the location of the mouse cursor was sampled at 60Hz; at every screen refresh, the x and y coordinates of the mouse were recorded. Mouse trajectories were screened such that any trajectories that moved below the starting point (i.e. contained coordinates with y values below -300), went 100 pixels to left or right of left and right targets respectively, or 100 pixels above the height of the target on the screens were excluded from this analysis as they resulted in substantial outliers. These trials amounted to 2.3% of total trials.

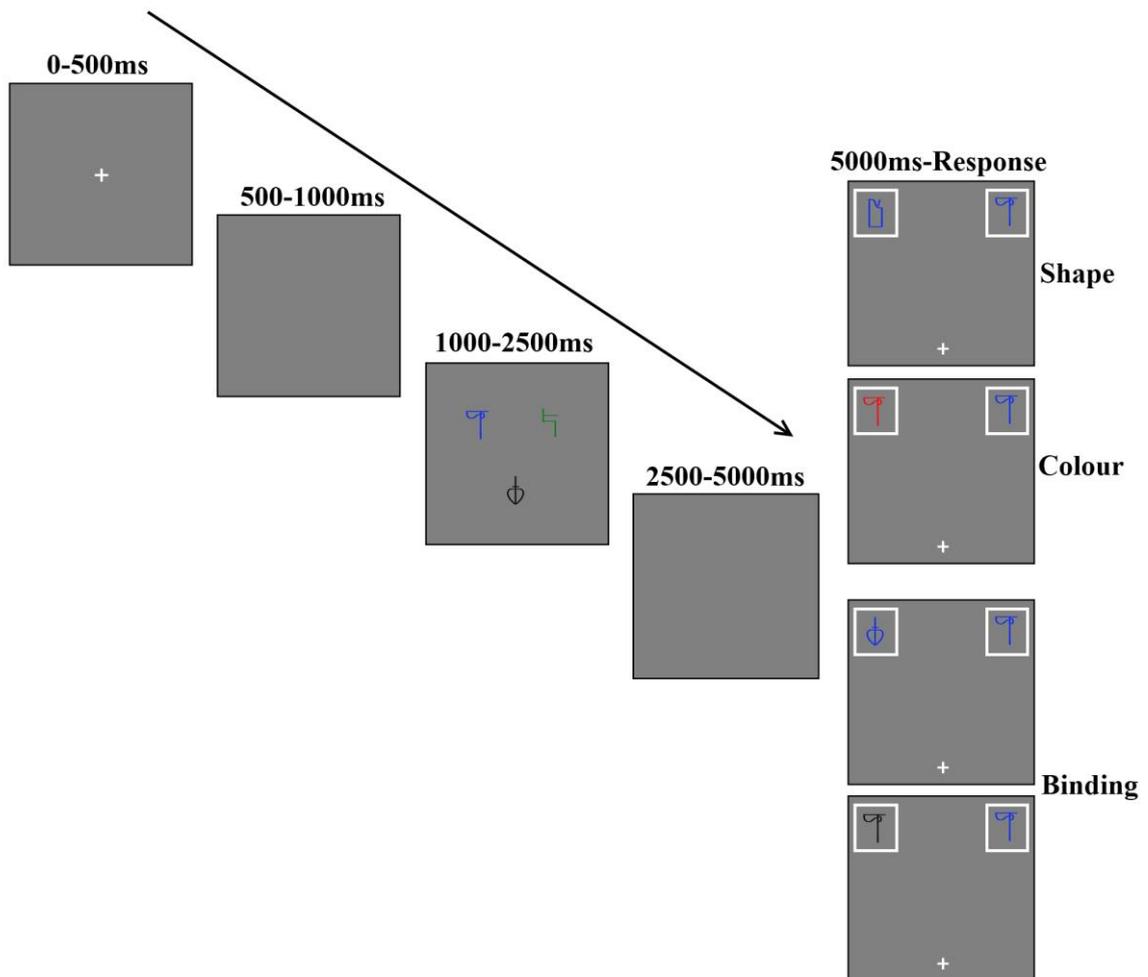


Figure 3.2. A schematic of the sequence of events in a trial showing the four types of test displays presented to participants (shown on the far right). The target is presented on right side in each case. In the top two examples, the lure contains novel visual features (novel condition) while the lures in the bottom two are recombinations of visual features from the memory display (binding condition). The fixation cross in the test displays represents the mouse cursor. Stimuli are not drawn to scale.

A repeated measures ANOVA was run to ensure that the proportion of excluded trials did not differ between binding, shape and colour conditions. The results showed this to be the case ( $p = .67$ ). For all trials in which the target was on the left, x coordinates were “flipped” (i.e. multiplied by -1) to remove location of target as a variable. To enable averaging of trajectories across trials and subjects, each trajectory was time normalised to 101 steps via a

process of linear interpolation. All trajectories were then space normalised so that the initial coordinate was transformed to 0,0 and the final coordinate was the centre of the box surrounding the target (250,600). For each condition, all x and y coordinates were pooled together and a heat map was created for each condition, showing the areas most commonly occupied by the mouse cursor (see [Figure 3.4](#)).

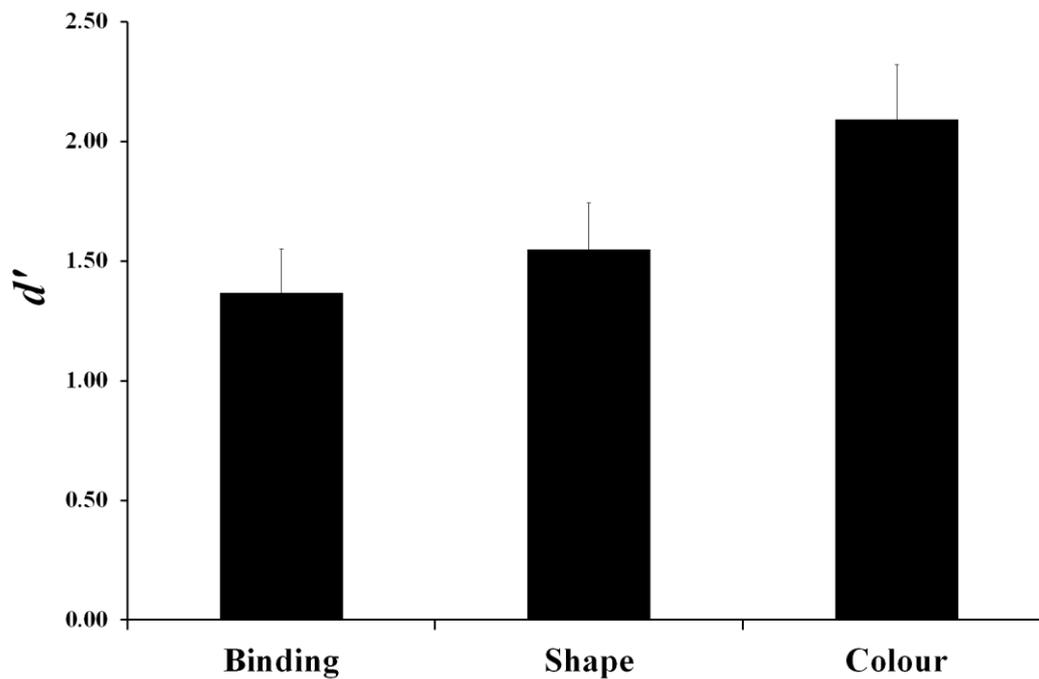


Figure 3.3.  $d'$  values across the three experimental conditions. Error bars show standard errors of the mean.

In addition, the mean location at each of the 101 time steps was calculated for each condition, allowing an average trajectory for each condition to be created. As shown in [Figure 3.5](#), trajectories for binding conditions had greater curvature than both colour and shape conditions. That is, movements started gravitating towards the target sooner for novel conditions than for binding conditions. To quantify this difference in trajectory curvature, the maximum displacement (in pixels), relative to an imaginary straight line drawn from the starting point of the trajectory to the centre of the target, was measured for each trial. This is a common measure of trajectory curvature (e.g. Freeman & Ambady, 2010; Hindy, Hamilton,

Houghtling, Coslett, & Thompson-Schill, 2009; McKinstry, Dale, & Spivey, 2008; Yu, Wang, Wang, & Bastin, 2012). Means were then calculated for each condition within each subject and then submitted to a one-way repeated measures ANOVA, which showed a significant effect of condition,  $F(2,34) = 7.46$ ,  $p < .005$ , partial  $\eta^2 = .305$ . As shown in Figure 3B, trajectories in the binding condition exhibited greater curvature than both shape and colour conditions. Importantly, planned pairwise comparisons showed both differences to be significant: colour vs. binding ( $p = .004$ ); shape vs. binding ( $p = 0.03$ ).

There are two possible — but not mutually exclusive — sources of the greater levels of curvature in the binding condition. It could be the case that the trajectories in this condition spend a greater period of time in regions roughly equidistant between target and lure. In this scenario, participants simply spend a greater period of time in an “uncertain” cognitive state, represented by locations in the middle of the screen. Alternatively, the binding condition could include a greater proportion of trials in which participants make movements toward the lure before reversing their decision and correctly selecting the target. The heat maps in Figure 3.4 provide preliminary evidence that the latter may apply to the current set of data; the area corresponding to the location of the lure (the top left of each figure) appears to have been occupied more often in the binding conditions than colour or shape conditions. To formally assess whether decision reversals are driving the differences in curvature between binding and visual feature conditions, a distributional analysis was performed to determine if trajectories in the binding condition exhibited greater levels of bimodality (Dale et al., 2007; Freeman & Ambady, 2010). For this analysis, shape and colour trials were combined to account for the difference in trial numbers between binding and visual feature conditions. This combined data will be referred to as the novel condition. In addition, all trials were summed across subjects as this analysis requires large numbers of data points (Dale et al., 2007). Maximum displacement values for each trial were calculated and then converted to z-

scores for novel and binding conditions. A histogram showing the distribution of z-scores for each condition is presented in [Figure 3.5 C](#), which clearly shows some evidence for bimodality in the binding condition, with a second, smaller peak occurring between 2 and 3 z-scores greater than the mean. Bimodality coefficients (SAS Institute, 1999) were calculated for each distribution, showing that the binding condition ( $b = .47$ ) exhibited greater levels of bimodality than the novel condition ( $b = .26$ ). A two-sample Kolmogorov–Smirnov test was performed to examine whether the two distributions differed significantly. The results showed this to be the case (*Kolmogorov–Smirnov*  $Z = 1.54$ ,  $p = .02$ ), suggesting that the increased curvature in the binding condition can be attributed, at least in part, to the greater number of decision reversals in that condition.

This does not preclude the possibility that, even in those trials where participants did not reverse their decision, trajectory curvature was greater in the binding condition due to a delay in evidence accumulation relative to the visual feature conditions. To test this possibility, all trials in which mouse movements gravitated towards the lure were excluded, and maximum displacement values were computed based on the remaining trials. Specifically, all trajectories that included x-values of less than -50 were removed (1/5<sup>th</sup> of the way towards the lure), leaving only those trials in which participants made a (relatively) straight upward movement before selecting the target. A one-way repeated measures ANOVA was performed to assess if there was an effect of condition for these trials. The result trended towards — but did not reach — significance,  $F(2,34) = 2.04$ ,  $p = .15$ , suggesting that the increased curvature in this set of results is primarily caused by the greater number of decision reversals in the binding condition.

A second variable of interest extracted from the mouse trajectory data was the number of directional changes along the x-axis during a trial — a measure of trajectory complexity (Dale & Duran, 2011; Dale, Roche, Snyder, & McCall, 2008). This measure provides an

additional index of competition between target and lure. When there is extensive competition between the two items (as predicted for the binding condition), mouse movements should exhibit small vacillations along the x-axis. Alternatively, smooth, uniform movements should be observed if evidence accumulation occurs rapidly, thereby resulting in minimal competition between the target and lure (as predicted for the visual feature conditions). The number of x-flips was calculated for each trial by counting the number of times mouse movements changed directions during the trial. A repeated measures ANOVA again showed a significant effect of condition,  $F(2,34) = 4.43$ ,  $p < .05$ , partial  $\eta^2 = .207$ , with the binding condition producing the most x-flips. As was the case with measures of curvature, planned comparisons showed that the binding condition produced significantly more x-flips than both shape ( $p = .013$ ) and colour ( $p = .011$ ) conditions — see [Figure 3.5 D](#). It is important to note that, while curvature and complexity both provide measures of competition between the target and lure, they do so in fundamentally different ways. Measures of curvature provide information about the degree to which a given trajectory occupies regions in between the target and lure, or regions closer to the lure than the target. Larger portions of a trajectory should be spent in these regions when the two options are in relatively strong competition for selection. Changes of direction along the x-axis, on the other hand, provide an index of competition on a much smaller scale; when competition between the two items is high, trajectories should exhibit fluctuations back and forth along the x-axis, independent of the mouse cursor's position on the screen. To test whether these two measures are, in fact, tapping into different phenomena, the mean maximum trajectory height (curvature) and number of x-flips (complexity) for all conditions within each subject were entered into a correlation. This analysis showed no evidence that the two measures were correlated ( $r = .195$ ,  $p = .157$ ).

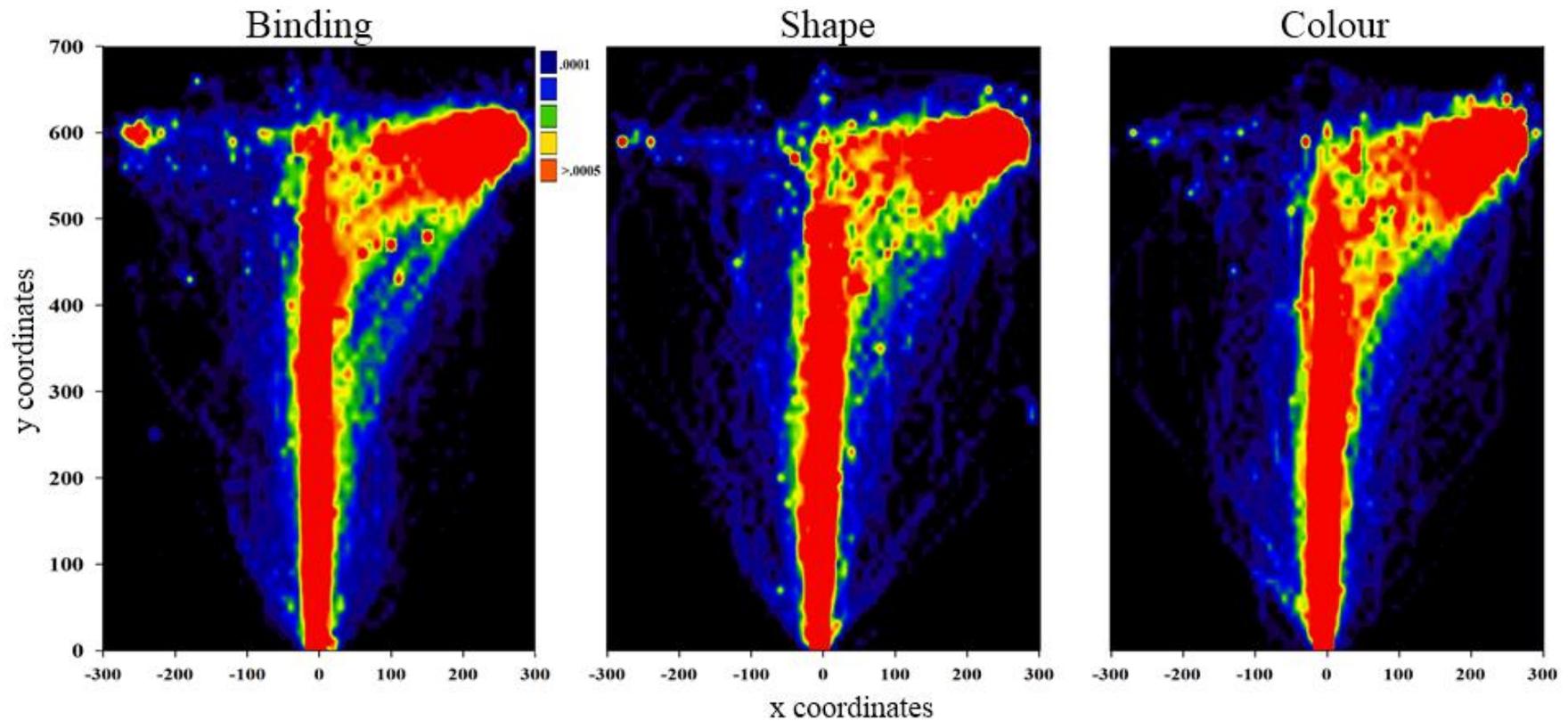


Figure 3.4. Heat maps showing the regions of space occupied most frequently occupied for (from left to right) the binding, shape and colour conditions. Heat maps were created by first dividing the area into 10x10 pixel squares, and then calculating the number of x,y coordinates occurring in each square. The raw count in each square was then converted to a proportion (see figure legend). That is, the count in each square was divided by the total count across all squares. This was done so that a common scale could be applied to each condition's heat map, given the differing number of trials (and, therefore, x,y coordinates) between conditions.

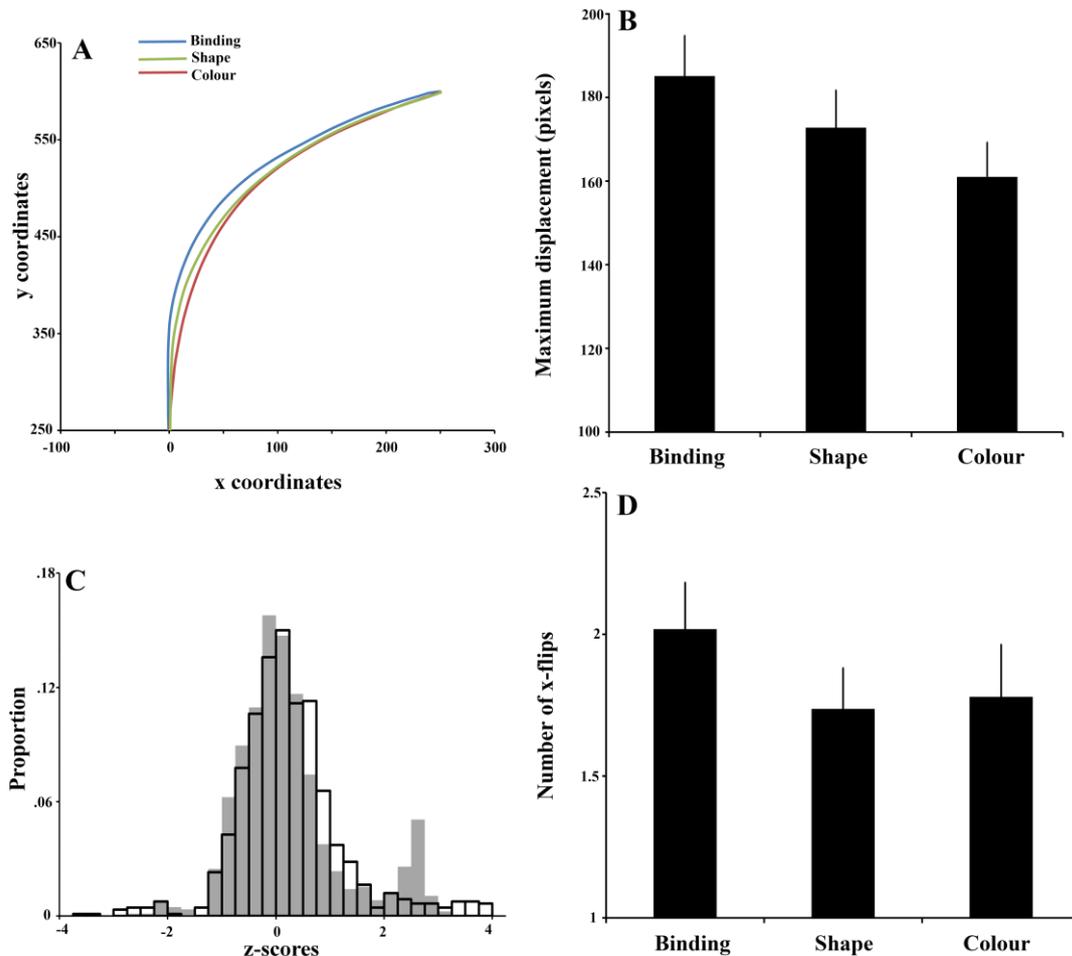


Figure 3.5. A summary of trajectory analyses. **A:** The upper portion of the trajectories for the three conditions averaged across all trials. The increased curvature associated with the binding condition is clearly illustrated here. **B:** Average maximum displacement values (a common measure of trajectory curvature) for the three conditions. Pairwise comparisons showed curvature to be significantly greater than both shape and colour conditions. **C:** Histogram showing the z-scores of maximum displacement values for binding and novel trials. Novel trials include trials from shape and colour conditions. Note the bimodality associated with the binding condition (shown in grey). **D:** Average number of x-flips made during a trial (a measure of trajectory complexity) for the three conditions. Planned comparisons showed significantly more x-flips during binding trials than both shape and colour trials. All error bars are standard errors of the mean.

### 3.3.3. Response times

Even though participants were not required to make speeded responses, response times were analysed to assess whether the effects observed in the mouse trajectory data were also captured by this more traditional measure of performance. While a main effect of condition was found,  $F(2,34) = 4.20$ ,  $p < .05$ , partial  $\eta^2 = .198$ , it was only the colour condition that produced faster response times than the binding condition ( $p = .022$ ). The difference between

shape and binding conditions did not approach significance ( $p = .352$ ). This suggests that a traditional experimental measure like response time is, in this case at least, blind to effects that can be captured by variables extracted from the recording of mouse movements during a trial.

### **3.4. General Discussion**

In the current study, a novel paradigm was used to investigate the representational format of visual working memory. It was novel in two respects: first, I manipulated the nature of the lure in a 2AFC task such that it either contained novel visual features (relative to the contents of working memory) or was a recombination of visual features maintained in working memory; second, participants responded by moving the mouse cursor to their selection, enabling online recording of mouse movements while a decision was being made. While the 2AFC task has recently been used (in addition to the change-detection task) to evaluate the capacity of visual working memory under different paradigms (Makovski et al., 2010), it has not as yet been used in the investigation of binding in visual working memory. There is a general consensus that equal performance for binding and novel feature conditions in change-detection tasks is evidence that binding and feature information are stored equally well in visual working memory, while reduced performance in the binding condition relative to novel feature conditions suggests that binding information is more easily lost (Allen et al., 2006; Delvenne & Bruyer, 2004; Fougne & Marois, 2009; Johnson et al., 2008; Poom & Olsson, 2009; Treisman, 2004; Ueno et al., 2011; Wheeler & Treisman, 2002; Yeh, Yang, & Chiu, 2005). The current study also adopted the rationale that comparing performance between binding and visual feature conditions informs models of binding in visual working memory, but increased the indices of performance beyond accuracy/sensitivity to include measurements of mouse movements that provide information about the decision process.

While  $d'$  values varied according to the nature of the lure in this set of results, these data provide only weak evidence for the feature-channel hypothesis. As noted by Johnson and colleagues (2008), this is because it is not clear how to interpret sets of results in which the binding condition produces accuracy/sensitivity scores worse than only a single visual feature condition. A conservative approach might be to accept as evidence for feature-channel hypotheses only those sets of results in which the binding condition is worse than *both* visual feature conditions. A compelling reason to reject this interpretation for the current set of results is that, as is the case for single-display change detection tasks, a confounding strategy is available to participants that could potentially inflate sensitivity in the binding condition relative to the visual feature conditions. That is, participants are able to correctly select the target in binding trials even if the target, for whatever reason, is not maintained in working memory. It is possible that if this strategy was controlled for — as has been done in previous work (Allen et al., 2006) — sensitivity in the binding condition would drop below both visual feature conditions. Regardless, it is certainly not the case that the sensitivity data reported here provide compelling evidence for the object hypothesis, as performance in the binding condition was the lowest of the three conditions as well as being significantly worse than performance in the colour condition.

While the sensitivity results may not be particularly compelling, the mouse movement data provided strong evidence that the decision process in the current experiment is mediated by the presence or absence of novel visual features in the test display. Specifically, increased competition (as indexed by trajectory curvature and complexity) exists between target and lure in the binding condition relative to *both* visual feature conditions. This is commensurate with a visual working memory representational system containing parallel visual feature channels, in which decisions can be made based on information *within* feature channels more readily than decisions requiring the binding of information *across* feature channels. This

interpretation postulates that any difference between binding and visual feature conditions can be attributed to the nature of visual working memory representations. This assertion requires a rebuttal to claims that this result could occur even if visual working memory maintains integrated representations.

There is considerable evidence that the contents of working memory bias the perception and attentional selection of visual stimuli (Soto, Heinke, Humphreys, & Blanco, 2005; Soto, Hodsoll, Rotshtein, & Humphreys, 2008; Soto, Humphreys, & Heinke, 2006). Particularly relevant to the current study, Soto and Humphreys (2009) have shown that even an irrelevant object feature (in this case, colour) biases feature based attentional selection. Participants were presented with a coloured object to maintain in working memory and were required to maintain only the shape (and not the colour) in memory. This was followed by a visual search task requiring the detection of a tilted line amongst vertical lines. Importantly, each line was surrounded by a coloured shape, with one of the distractors being surrounded by an object that either matched the memory item's colour, its shape, or both (conjunction condition). The results showed that participants often made their first saccade not towards the target, but towards the distractor surrounded by an object sharing visual features with the memory item. The number of these saccades was equivalent between colour and conjunction conditions, suggesting that, even though colour was not required for the memory task, it was nonetheless encoded in working memory and subsequently biased perceptual processing of the search array towards items that contained the colour of the item in memory.

One interpretation of this result, with potential implications for the current study, is that while visual working memory maintenance is object based (as shown by the irrelevant visual feature being encoded into working memory), it is nonetheless able to bias the perceptual processing of individual visual features. This facilitation of the perceptual processing of visual features maintained in working memory could explain the difference in mouse

trajectories observed in the current study. There are, however, a number of problems with this interpretation. First, the finding of Soto and Humphreys (2009) that task irrelevant visual features can have behavioural effects does not speak to the issue of working memory maintenance per se, but to encoding. That is, it could be the case that committing an item to working memory results in all the visual features associated with that item being encoded — whether these features are maintained in parallel feature channels or together in object based slots is a distinct issue. Second, some aspects of the Soto and Humphrey's (2009) study cast doubt on the relevance of their findings to the current experiment. For example, the search array was presented a mere 188ms after the memory item, an ISI usually associated with iconic memory as opposed to the more durable working memory. Indeed at longer ISIs, irrelevant visual features associated with a memory item have been shown not to guide feature-based visual search (Olivers, Meijer, & Theeuwes, 2006). Furthermore, Soto and Humphreys required participants to maintain only a single item in memory, while the set size in the current study was three items. This is important because the memory guided, feature based attentional selection does not occur when more than one item is maintained in working memory (Downing & Dodds, 2004; Houtkamp & Roelfsema, 2006; Soto & Humphreys, 2008). It is therefore unlikely that the current set of results can be explained by integrated representations biasing the processing of individual visual features.

It has been shown that participants are able to select which features of objects are encoded into working memory (Olivers et al., 2006; Serences et al., 2009; Woodman & Vogel, 2008; Xu, 2002, 2010). This raises the possibility that participants employ a strategy of prioritising the encoding of visual features present in the test display at the expense of encoding binding information. This strategy would also produce the result of less competition between target and lure for visual feature conditions (as indexed by the mouse movement results). This explanation is unlikely however, as accuracy in the binding condition was considerably above

chance, suggesting that binding information was sufficiently encoded. In addition, accuracy in the binding condition was not significantly lower than the novel shape condition, making it unlikely that participants were simply prioritising the encoding of visual features relative to binding information.

Participants could also have adopted a decision strategy in which they first make a decision based on the presence of a novel visual feature and if not, selecting the object with the correct colour-shape combination. Such a strategy would also result in greater levels of curvature for the binding condition, as participants make movements towards the target in the visual feature conditions sooner than is the case for the binding condition. While the current set of data cannot rule out this decision strategy account, there is some evidence to suggest that it is unlikely, as the increased curvature in the binding condition was due not to a delay in selecting the target, but because participants incorrectly moved the cursor to the lure most often in the binding condition.

The interpretation advocated here — that the increased competition in the binding condition is due to a feature based representational format in working memory — is based on the assumption that the current 2AFC task involves the independent comparison of target and lure with information maintained in visual working memory, that the relative memory strengths of each item gives rise to competition for selection between the target and lure, and that this competition can be observed by the recording of mouse movements during a trial. There were two sets of results that suggest greater levels of competition in the binding condition compared to both visual feature conditions: mouse trajectories were more curved in the binding condition (due to participants moving the mouse towards the lure more often in this condition) and mouse trajectories changed direction more often in the binding condition. The increased competition in the binding condition does not easily lend itself to an object-based account of visual working memory, as the lure in both binding and visual feature

conditions do not match an integrated object in working memory. Instead, the results presented here suggest that decisions based on visual features produce less competition in the current 2AFC task — evidence that the fundamental units of visual working memory are visual features, not integrated objects.

Finally, this feature-channel account is compatible with recent neuroscience data that proposes visual-feature specific working memory stores in posterior visual regions. Cognitive models of visual working memory representation must be consistent with results from the cognitive neuroscience community, and it is difficult to reconcile object based accounts with a neural account that involves separate brain areas maintaining different visual features.

## **Chapter 4: Study 3 – Determining the source of the binding deficit in visual working memory**

### **4.1. Introduction**

Visual working memory, as evidenced by a body of research from both primate and human studies, is strongly dependent on processes in the prefrontal cortex (Goldman-Rakic, 1987), although there is considerable debate as to the functional significance of this prefrontal activity. While some regard prefrontal activity to reflect the active storage of visual information (Courtney, 2004; Goldman-Rakic, 1987; Smith & Jonides, 1999), a recent hypothesis (the sensory recruitment model) suggests that it reflects processes which, via top-down signals, maintains posterior perceptual regions in an active state (D’Esposito, 2007; Postle, 2006; Ranganath et al., 2004). This latter proposal regards the storage of visual information in working memory as simply the prolonged activation of perceptual regions of the brain — as opposed to the information being maintained in a specialised buffer located in the frontal lobes — and is similar in many respects to the *coherence theory* of visual attention proposed by Rensink (2000), which regards visual working (or short-term) memory as the interaction between higher-level, attentional processes and lower-level visual features. An important feature of the sensory recruitment model is that the distributed nature of representation in visual perception extends to visual working memory. That is, the feature-specific, modular organisation of the visual system (Tootell et al., 1996) carries over to the maintenance of visual information in working memory (Slotnick, 2004).

The findings supporting this neural model of visual working memory maintenance have important implications for the debate between cognitive models of visual working memory representation, in which there are two broad camps. Proponents of the object account of visual working memory propose that visual memory maintains integrated, fully-bound representations in an all-or-none fashion (Luck & Vogel, 1997). The feature-channel account

(Wheeler & Treisman, 2002), on the other hand, posits independent visual feature channels, each storing different visual features (colour, shape, orientation etc.). The feature-channel account, does not, however, suggest that visual features are necessarily “free-floating”. Instead, visual features from the same object are bound together by associative links. The important distinction between these two rough models is that only the feature-channel account allows for individual visual features (or feature-feature associations) to be lost from memory without compromising the maintenance of all the feature information pertaining to a particular object.

Behavioural evidence for the feature-channel account derives largely from two paradigms. Recently, mixture modelling methods, have shown that visual features are maintained (and lost) independently from each other (Bays et al., 2011; Fougne & Alvarez, 2011). In the experiments reported by Bays et al. (2011), participants were provided with a display of oriented bars of different colours to maintain in working memory. After a delay period, a single item was presented at one of the original locations, and participants turned two “dials” that changed the item’s orientation and colour until it matched the original item along both visual feature dimensions. The key contribution of this paradigm is that it models errors as occurring in two distinct ways: variability in memory for the target (based on a Gaussian distribution) and a uniform distribution corresponding to random guesses. By collecting responses for both features, this paradigm is able to determine whether the distributions of errors for both features are highly correlated (as expected by the object account), or whether visual features fail independently of each other. The results were largely supportive of the latter proposal. More commonly, however, the paradigm of choice in studies investigating this topic is the change-detection task, producing mixed results. Wheeler and Treisman (2002), as well as Chapter 2 of the current thesis, have shown that detecting a change involving a swapping of visual features (a binding change) is more difficult to detect than

changes involving the addition of novel visual feature values (although see Johnson, Hollingworth, and Luck (2008) for a qualification of Wheeler and Treisman's results). Importantly, this effect is only apparent when multiple items are presented in the test display and not when a single item is presented (Wheeler & Treisman, 2002).

There are two competing hypotheses to explain why presenting multi-item test displays specifically disrupts binding in working memory. According to Wheeler and Treisman (2002), it is the recruitment of attention in processing the multiple items of the test display that causes binding information to be lost in visual working memory. That is, the maintenance of binding information is contingent on attention being focussed on working memory representations; when attention is diverted away from these representations to the perceptual processing of the multiple items in the test display binding fails in working memory. Allen, Baddeley, and Hitch (2006) have proposed an interference account to explain why binding may fail more readily than visual features in visual working memory upon presentation of a multi-item test display. This account suggests that while binding is automatically maintained in working memory, it is grounded in representations that are more fragile and prone to interference than those underlying working memory for visual features. According to this account, whole displays would simply result in more interference than single displays, causing a greater loss of binding information than is the case for single displays. That is, the subtle difference between these accounts rests on whether attention is required to be directed towards memory representations for the successful maintenance of binding information.

Direct experimental investigations of the attentional hypothesis have largely failed to support the notion that attention has a special role in maintaining binding information in visual working memory. One way of assessing attention's role in maintaining binding information in working memory is to manipulate the extent to which attention is allocated to

individual items in working memory. Gajewski and Brockmole (2006) used such a rationale in their investigation of the relationship between attention and binding in visual working memory. Instead of a change-detection task, however, they used an explicit recall paradigm that involved cueing individual items in working memory. Participants were presented with an initial display of six coloured shapes, followed by a short delay (507 ms) and then a spatial cue, which signalled participants to attend to the cued item in working memory. After a second short delay (347 ms), a probe was presented at one of the initial display locations and participants were required to report the shape and/or colour of the item corresponding to the probe. In valid trials, the probe was at the same location as the cue; in invalid trials, the probe was at a different location. The authors reasoned that if attention is required to maintain binding information in working memory, then withdrawing attention from an item in working memory, as occurs in the invalid condition, should result in the independent recall of each shape and colour. Instead, the results showed that in the invalid condition, participants tended to either recall both visual features or none at all. This finding contradicts the notion that when attention is withdrawn from items in working memory, binding information fails more readily than feature information.

Similarly, Delvenne, Cleeremans, and Laloyaux (2010) have used a retroactive cue to determine the benefit gained in change-detection performance when two items are cued in working memory prior to the onset of the test display. The authors hypothesised that, if attention is required to maintain binding information but not visual feature information in working memory, then cueing should only benefit novel visual feature changes but not binding changes. The rationale is that since attention is already focussed on binding information, cueing should cause no benefit in performance for binding changes. The maintenance of visual feature information, on the other hand, does not, according to Wheeler and Treisman's attentional hypothesis, require sustained attention to be maintained in

working memory. As such, cueing should cause an increase in performance for novel visual feature changes. Contrary to this proposal, the authors found no evidence for a differential benefit of retro-cues across binding and novel visual feature conditions over a series of experiments. That is, cueing items in working memory resulted in an equivalent increase in change-detection performance for both novel and binding changes (relative to conditions in which no items were cued in working memory). There are, however, a number of flaws with this study, the discussion of which requires a closer examination of the methodology employed.

The basic design of the experiments followed a factorial design with condition (shape/colour/binding) as one factor and cuing (cued/uncued) as the other. The test display was a single item. In the cued version of the tasks, two items from the initial display were cued. The cues were 100% informative, in that participants were made aware that if there was a change, it would always involve a cued item. All three conditions were blocked, which meant that there were differential encoding demands between the conditions. Namely, participants only had to encode and maintain a single visual feature dimension in the two feature conditions, while they had to encode two feature dimensions<sup>17</sup> (and their associations) in the binding condition. Accordingly, it is difficult to attribute any significant effects (or lack thereof) to encoding or maintenance. This difference in encoding demands is compounded by a second flaw. When two items are cued in the binding condition, a change trial involved the two cued items swapping visual features. A consequence of this is that detecting all possible changes in this condition only requires shifting attention to a single item in working memory, not both cued items. For example, if a red square and a blue circle are cued, participants can detect all possible changes (red circle, blue square), by simply shifting

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<sup>17</sup> Visual feature dimensions here refer to basic visual properties usually associated with the term “visual features” e.g. orientation, colour, shape etc. Visual feature values refer to specific values within each dimension e.g. red, blue, yellow etc.

attention to only the red square in working memory<sup>18</sup>. This strategy is not possible for novel visual feature changes. This is particularly important as Makovski and Jiang (2007) have shown that cueing one item in working memory produces benefits in change-detection performance to a far greater extent than cueing of two items, whether the cues are presented centrally or peripherally. Taken together, these confounds cast doubt on the findings and interpretation of Delvenne et al.(2010).

A second method of investigating the role of attention in working memory is to present an attentionally demanding secondary task in the delay period of a change-detection task. This has been used in a number of studies with mixed results. Yeh, Yang and Chiu (2005) required participants to make a speeded vowel/consonant judgement to a single letter, presented centrally or peripherally, in the delay period of a change-detection task. The authors found that, while the peripheral condition (which presumably placed the strongest demands on attention) reduced change-detection performance, it did so equally for novel colour and binding conditions, suggesting that attention does not play a special role in the maintenance of binding information. There are, however, two issues with this experiment that detract from its contribution to the debate about the role of attention in binding visual features in working memory. First, the memory items were composed of only a single relevant visual feature dimension (colour) and the binding condition involved colours swapping locations. As such, these results are only relevant to colour-location binding. Second, the results of this study are based on hit rates even though, as Johnson et al. (2008) point out, there appears to be substantial variation in correct rejection rates in the study.

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<sup>18</sup> One way of getting around this might be to have the cued item swap visual features with one of the uncued items. The problem with such a design, however, is that it is not clear if such a change qualifies as a binding change. If the uncued items are lost from working memory, then swapping visual features with these items would be functionally equivalent to a novel visual feature change i.e. the test display would involve the addition of visual features not present in working memory.

Allen et al. (2006) tested the attentional hypothesis by presenting a range of attentionally demanding secondary tasks during change-detection tasks. Backwards counting in steps of both one and three — tasks known to require executive, attentional resources (Han & Kim, 2004; Postma & De Haan, 1996) — during the delay period did not disrupt performance in binding conditions significantly more than shape or colour conditions. In addition, the authors assessed the role of executive function in maintaining binding information in working memory by requiring participants to perform a concurrent verbal memory task. In the dual-task condition, participants were sequentially presented with a string of six digits to remember before each change-detection trial. They were then required to recall the digits (in the correct order) during the presentation of the initial display and the delay period. As was the case for the backwards counting secondary tasks, this manipulation did not specifically disrupt binding information in working memory. The authors then assessed the role of interference in disrupting binding information by comparing performance in a standard change-detection task with a version of the task in which the memory items were presented sequentially (but still in different locations). The difference between novel and binding conditions should be greater in the sequential version of the task if the interference produced by the presentation of subsequent items is especially disruptive of binding information in working memory. Additionally, the difference between binding and novel changes should be greatest for items presented earlier in the rapid serial visual presentation sequence (RSVP), as these items should undergo greater levels of interference than those presented towards the end of the RSVP sequence. This is precisely what Allen and colleagues (2006) found, causing them to conclude that interference — and not the reallocation of attention from working memory to perception — played a major role in disrupting visual working memory for binding information.

The secondary tasks used by Yeh et al. (2005) and Allen et al. (2006) probed a general, amodal form of attention, but it is possible that visual attention in particular is necessary for the maintenance of binding in visual working memory. To this end, two studies — using the same rationale as Yeh et al. (2005) and Allen et al. (2006) — have presented a secondary task in the delay period that requires visual attention. The first was by Johnson et al. (2008) and included a secondary task that consisted of the presentation of four pairs of square outlines, with each pair presented in four corners of the screen. Each shape contained a gap that pointed in one of the four cardinal directions. Only one shape (out of eight) opened to the left or the right of the screen (all others pointed up or down), and the participants' task was to make a left or right response depending on which direction this search target was pointing. Visual search tasks using these stimuli have previously been shown to require sequential shifts of attention (Woodman & Luck, 2003). If sustained visual attention is required to maintain binding information in visual working memory, the search task should cause a larger decrease in performance for binding conditions than for novel visual feature conditions. While the search task did disrupt performance, it did so across all conditions to similar degrees, suggesting that the attentionally demanding search task did not disrupt binding in working memory any more than was the case for visual features.

A similar study was performed by Fougny and Marois (2009), who used multiple object tracking as the attentionally demanding secondary task. In this secondary task, twelve stationary discs were presented to the participant. Nine were hollow white discs, while three were filled in white, indicating that these three were targets to be attended to (the marker phase). After 2000ms, the white fill of the targets were removed (i.e. all twelve discs were now hollow) and all discs began moving in random directions for 3000ms (the tracking phase). Finally, one of the twelve discs was filled with white, and participants were required to respond if the filled disc corresponded to one of the initial targets (the probe phase). Unlike

the aforementioned studies, this task was shown to specifically reduce performance in the binding condition relative to novel shape and colour changes. Importantly, this was not the case when participants were presented, as a control condition in experiment 1 of their study, with a multiple object tracking display without the requirement to track individual items i.e. they did not attend to the display. In addition, the control secondary task in experiment 2 that involved encoding and retrieval (the marker and probe phases), but replaced the tracking phase with a static display did not affect binding more so than novel visual feature changes.

It is not clear, however, whether this finding is supportive of the attentional account of Wheeler and Treisman (2002) or of the interference account of Allen and colleagues (2006). That is, it is not clear if binding fails in these tasks because attention is diverted away from working memory representations to the perceptual task of tracking multiple objects, or if the tracking task simply interferes with intrinsically fragile binding representations maintained in working memory. In other words, it could be the act of attending to the display or the process of tracking that disrupts binding in working memory. These two processes, while no doubt highly related, have been shown to recruit differential neural resources. Howe, Horowitz, Morocz, Wolfe and Livingstone (2009) have shown that a group of regions in posterior parietal cortex, as well as regions MT and the frontal eye fields are activated more by the act of tracking moving objects than simply attending to objects. This fits with the finding in experiment 2 of Fougnie and Marois (2009) that attending to a stationary image of discs did not specifically disrupt binding in working memory. Perhaps then, the findings of Fougnie and Marois (2009) are best interpreted in the framework of the interference account of Allen et al. (2006). Specifically, the act of tracking multiple objects is likely to be the critical process which disrupts the fragile binding representations in working memory.

To summarise, performance in binding conditions has been shown in chapter 2 of this thesis — as well as in previous research (Wheeler and Treisman, 2002) — to be worse than

novel visual feature conditions in change-detection tasks when the test display consists of multiple items, when the items in the initial display are presented sequentially (Allen et al. 2006) and when a multiple object tracking task is performed in the delay period of the change-detection task (Fougnie and Marois, 2009). What processes common to these experimental manipulations could specifically disrupt binding in working memory? It could be the case that multi-item test displays (relative to single-item test displays), the sequential presentation of items in the initial display at different locations (relative to static initial displays) and multiple object tracking secondary tasks (relative to a static secondary task) all require a greater number of eye movements before a response is made. Perhaps it is this increase in eye movements that specifically disrupts working memory for binding information in these different experimental manipulations. Indeed, a number of studies have shown that eye movements disrupt visual working memory for location information (Lawrence, Myerson, & Abrams, 2004; Lawrence, Myerson, Oonk, & Abrams, 2001; Postle & Hamidi, 2006), which may play an important role in the initial formation of feature-feature bindings in working memory (Jaswal & Logie, 2011; Logie et al., 2011; Treisman & Zhang, 2006). Location information is not important for feature binding in working memory when delay periods are greater than ~1000ms (Logie et al., 2011), calling into doubt whether eye movements are the primary causal factor driving the interference of feature binding in working memory. In addition, the attentionally demanding secondary task of Johnson et al. (2008) described earlier required eye movements but did not result in the differential loss of binding information.

It could also be the case that the source of interference in these manipulations is simply the greater amount of visual information that is processed relative to their individual control conditions. This *general interference* account is compatible with the neuroscience literature highlighting the role of posterior visual regions in maintaining visual information in working

memory (Pasternak & Greenlee, 2005; Serences et al., 2009; Slotnick, 2004). It is easy to imagine how the sharing of a common neural workspace between visual perception and visual working memory would lead to the increased interference of visual working memory when the amount of perceptual information entering this workspace increases. Furthermore, the working memory representations maintained during the delay period of a change-detection task should be particularly sensitive to multi-item test displays as these displays contain information that corresponds to the visual feature dimensions being maintained in working memory. That is, memory representations containing, for example, colour and orientation information should be most prone to interference by perceptual information that also contains colour and orientation information. This is because, as Slotnick (2004) has highlighted, the feature based modularity observed in visual perception carries over to working memory maintenance, which would mean that the regions maintaining information in visual working memory during the delay period are precisely the regions activated by the information in the test display. As binding information is proposed to be more fragile than visual feature information (Allen et al., 2006), this interference in the shared neural workspace would cause greater disruption of binding information in working memory.

Another possibility, not previously investigated in the literature, is that the critical process which disrupts binding in visual working memory during these manipulations is the *perceptual* binding of visual features (i.e. the process of binding visual features in the act of perceiving the test display). This process is necessarily more intensive when multiple items are presented in the test display than when a single item is presented. This is also compatible with the findings of Allen et al. (2006) involving the sequential presentation of memory items, which showed that items presented earlier on in the sequence were more likely to suffer from the loss of binding information, possibly due to the increased number of “bindings” that had to be performed by the visual system upon presentation of items later on

in the sequence. Finally, perceptual binding (namely, the binding of location and identity) is one of the important processes underlying successful multiple object tracking (Botterill, Allen, & McGeorge, 2011; Oksama & Hyönä, 2008). This *binding interference* hypothesis also relies on the very specific nature by which visual regions of the brain are recruited by both perception and working memory. According to this hypothesis, regions involved in perceptual binding are also recruited in the maintenance of binding information in working memory. Indeed, posterior parietal regions have been shown to be sensitive to conjunction visual search tasks (Donner et al., 2002; Wei, Müller, Pollmann, & Zhou, 2011), multiple object tracking tasks (Howe et al., 2009; Jahn, Wendt, Lotze, Papenmeier, & Huff, 2012; Jovicich et al., 2001) — both of which require perceptual binding — as well as tasks that require the maintenance of multi-dimensional items (Kawasaki, Watanabe, Okuda, Sakagami, & Aihara, 2008; Xu, 2007) or colour-location binding (Todd & Marois, 2004) in working memory.

The current study seeks to distinguish between these two interference accounts. It is based on experiment 1 of Johnson et al. (2008), in which participants were presented with a secondary visual search task in the delay period of a change detection task. The important difference is that the two visual search tasks described here involve stimuli that contain the same visual feature dimensions that are maintained in visual working memory. In both versions of the search task, participants were presented with pairs of coloured letters and required to search for an “odd pair out”. In the *pop-out* version of this task, this pair was defined by colours and letters entirely different from the other pairs and did not require perceptual binding, while in the *conjunction* version the odd pair out contained the same letters and colours as the other pairs, but involved different colour-letter associations and therefore did require perceptual binding to complete the task. If the general interference account is true, both versions of the task should disrupt binding information relative to visual

features in working memory, as both versions of the task require the perceptual processing of visual feature dimensions maintained in visual working memory during the delay period. If the binding interference account is true, however, then only the conjunction visual search task should disrupt binding in visual working memory. If neither search task specifically disrupts binding information in working memory, then the interference account of Allen and colleagues (2006) would be placed under serious doubt. Instead, this would be supportive of a strong object-based account of visual working memory in which information is maintained in the form of integrated representations. In such a framework, the storage of an object in working memory is all-or-none, and does not allow for visual features to be maintained if the associative links between these features is lost.

## **4.2. Method**

### **4.2.1. Participants**

16 participants (8 males; 15 right-handers) between the ages of 20 and 42 (mean age of 27.8) took part in the experiment.

### **4.2.2. Stimuli**

7 letters (D, F, G, J, K, P and Y) and 7 colours (white, red, blue, green, yellow, violet and brown) were used to create the stimuli. All stimuli were the same size as in experiment 1. The set size for memory task was three letters. The locations of the three letters randomly varied from trial to trial, with the restriction that the letters were placed 120° from each other around an imaginary circle subtending 6.1° of visual angle in the initial display. The test display was a single item in the centre of the screen.

Visual search stimuli consisted of four pairs of coloured letters, with each pair surrounded by a black box (see [Figure 4.1](#)). Each box subtended a visual angle of 2.8° and distance from

the centre of each box to the centre of the screen was  $9.5^\circ$  (viewed from 57cm). The colours and letters used in the visual search display were not present in either the initial or test displays.

### **4.2.3. Procedure and Design**

There were three types of change-detection conditions in the experiment: novel colour, novel letter and binding. The two novel conditions were always presented in the same block, with binding changes presented in separate blocks. The visual search tasks involved participants determining which side of the screen (left or right) contained the “odd pair out”: in the pop-out version of the task, the odd pair out consisted of a novel letter and a novel colour not present in the other 3 pairs; in the conjunction version of the task, the odd pair out contained different letter-colour bindings compared to the other three pairs. The location of each pair in the search tasks was randomised, with the two letters appearing  $180^\circ$  apart around an imaginary circle, centred in each black box and subtending  $1.81^\circ$ . In those blocks where no search task was presented, participants were presented with 4 empty boxes (see [Figure 4.1](#)).

There were 6 blocks in total: a binding and novel block with no search task presented in the delay period; a binding and novel block with the pop-out search task presented in the delay period; a binding and novel block with the conjunction search task presented in the delay period. All binding blocks were 36 trials (18 change trials/18 no-change trials), while all novel blocks were 72 trials (18 novel letter change trials/18 novel colour change trials/ 36 no-change trials), for a total of 324 trials. For blocks with no search task, there were 8 practice trials; for blocks with a search task, there were 4 practice trials of just the change-detection task, 4 trials with just the search task and finally 8 dual-task trials. The sequence of blocks was such that half the participants did the novel change blocks first, while the other half did all the binding

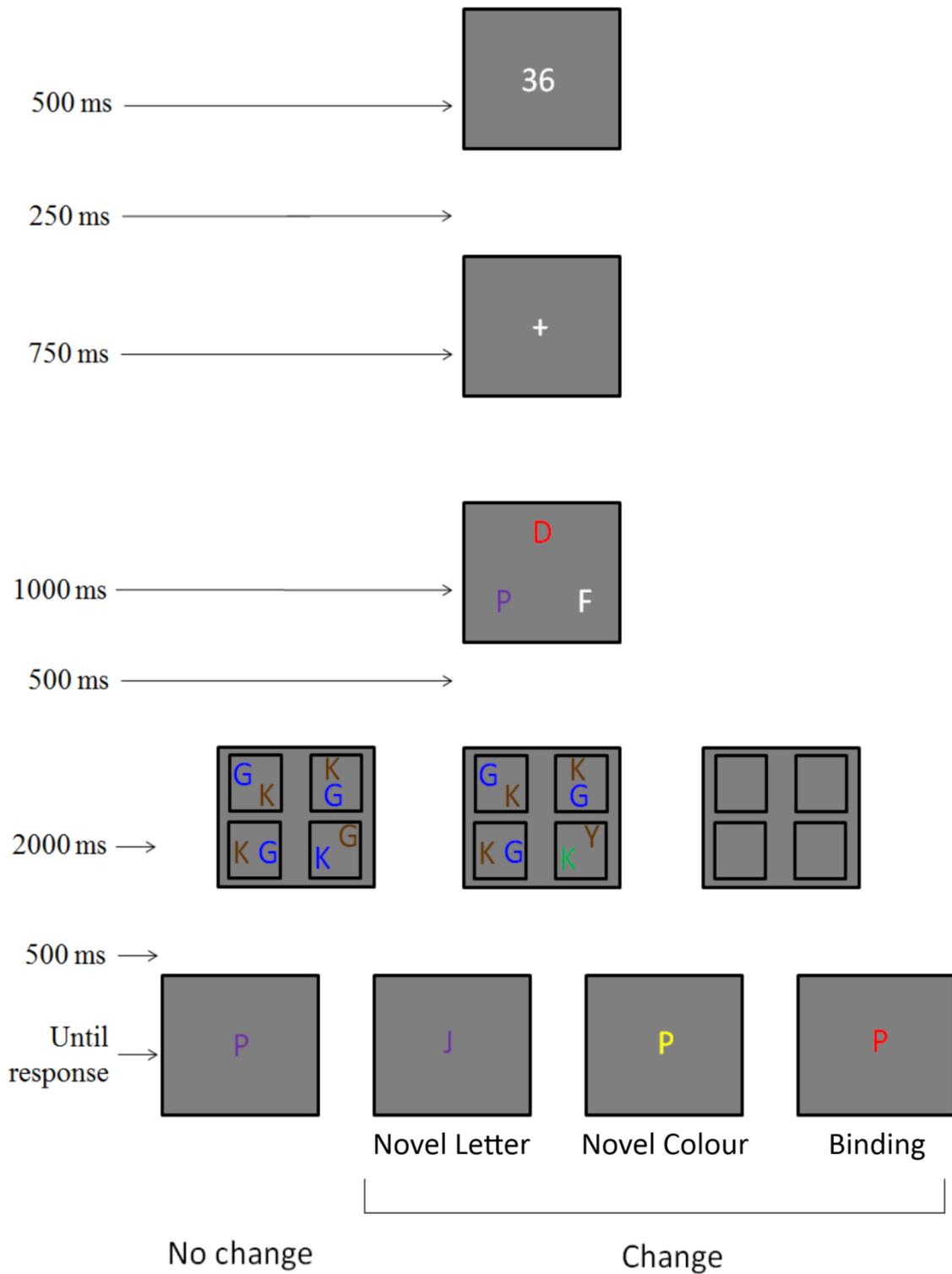


Figure 4.1. A schematic of the sequence of events in Experiment 2. 500ms after the offset of the initial display, one of three types of displays were presented: a conjunction visual search task, a pop-out visual search task or a display of empty boxes not requiring a response (the no search condition) — these are shown from left to right . After a short delay, a test display was presented, which stayed on the screen until participants responded.

blocks. The sequence of novel blocks was randomised for each participant — likewise for binding blocks.

As shown in [Figure 4.1](#), the task followed a standard change-detection paradigm, with the exception that in four of the blocks participants were presented with an array of four pairs of coloured letters during the delay period, and were instructed to respond, using the left and right mouse buttons, which side of the screen contained the odd pair out of the four. If a participant failed to respond before the offset of the visual search display, the search task for that trial was recorded as a miss (i.e. incorrect). In blocks where no search task was presented, participants made no responses in the delay period. Once the test display was presented, participants had to respond (also using the mouse buttons) whether the item had changed from the initial display (left button for no-change, right button for change). Response times for the change-detection responses were not recorded, and participants were instructed to favour accuracy over speed in this portion of the task.

As in experiment 1, articulatory suppression was employed to suppress verbal coding of stimuli

### **4.3. Results and Discussion**

#### **4.3.1. Visual search results**

Accuracy (proportion correct) and response times were analysed in a 2(*visual search task*: pop-out/conjunction) x 2(*change-detection task*: novel/binding) repeated measures ANOVA.

The visual search results are displayed in [Figure 4.2](#). There was a significant main effect of *visual search task* for proportion correct scores,  $F(1,15)=40.08$ ,  $p < 0.001$ , partial  $\eta^2 = 0.728$ , with higher scores observed in the pop-out condition ( $M = .97$ ) than the conjunction

condition ( $M=.88$ ). There was neither a significant effect of *change-detection task* ( $p=1.000$ ) nor a significant interaction ( $p=.286$ ). These results were mirrored in the analysis of response times (of correct responses only). The main effect of *visual search task* was strongly significant,  $F(1,15)=320.12$ ,  $p < 0.001$ , partial  $\eta^2 = 0.955$ ; responses were much quicker in the pop-out condition ( $M = 814.24\text{ms}$ ) compared to the conjunction condition ( $M = 1389.09\text{ms}$ ). Again, there was no effect of *change-detection task* ( $p=.519$ ), nor was the interaction significant ( $p=.370$ ).

### **4.3.2. Change-detection results**

Change-detection performance is shown in [Figure 4.3](#), and was analysed with a 3(*visual search task*: no search/pop-out/conjunction) x 3(*change-detection task*: novel colour/novel letter/binding) repeated measures ANOVA. For those conditions which involved dual-task trials, only those trials with correct responses to the visual search task are included. As in experiment 1, the measure of change-detection performance reported is  $d'$ , although all effects reported here were also apparent for the measures of  $A_z$  and corrected recognition.

Not surprisingly, a main effect of *visual search task* was found,  $F(2,30) = 59.51$ ,  $p < .001$ , partial  $\eta^2 = .799$ , with performance in the no search conditions ( $d' = 2.03$ ) being greater than the pop-out search conditions ( $d' = 1.07$ ) and conjunction search conditions ( $d' = .75$ ). While performance in the binding conditions ( $d' = 1.15$ ) were generally lower than novel letter ( $d' = 1.45$ ) and novel colour ( $d' = 1.25$ ) conditions, the effect of *change-detection task* was not significant ( $p=.15$ ). Importantly for the current study, a significant interaction was observed ( $F(4,60) = 3.82$ ,  $p < 0.01$ , partial  $\eta^2 = .203$ ), showing that any difference in performance between change-detection conditions was not the same across the three visual search tasks. As shown in [Figure 4.3](#), the difference between novel and binding conditions is only present when participants were required to perform a conjunction search. Pairwise comparisons

showed that detecting binding changes after performing the conjunction visual search task was significantly worse than both novel colour ( $p=0.008$ ) and novel letter ( $p = 0.027$ ) changes (uncorrected  $p$ -values).

To ensure that only the conjunction search task specifically disrupted binding in visual working memory, two simple effects analyses were performed comparing separately the effects of the conjunction and pop-out search tasks on performance (relative to the no-search condition), making for two  $2(\text{visual search task: no search/search}) \times 3(\text{change-detection task: novel colour/novel letter/binding})$  repeated measures ANOVAs. While the interaction was significant for the conjunction search analysis ( $F(2,30) = 5.65$ ,  $p < .01$ , partial  $\eta^2 = .274$ ), this was not the case for the pop-out search analysis ( $p=.213$ ).

The fact that performing a pop-out search in the delay period does not differentially affect binding in visual working memory is strong evidence that the source of this binding deficit caused by the conjunction visual search task is not simply due to *any* visual interference. Rather, it supports the hypothesis that the perceptual binding of visual features specifically disrupts binding information in visual working memory.

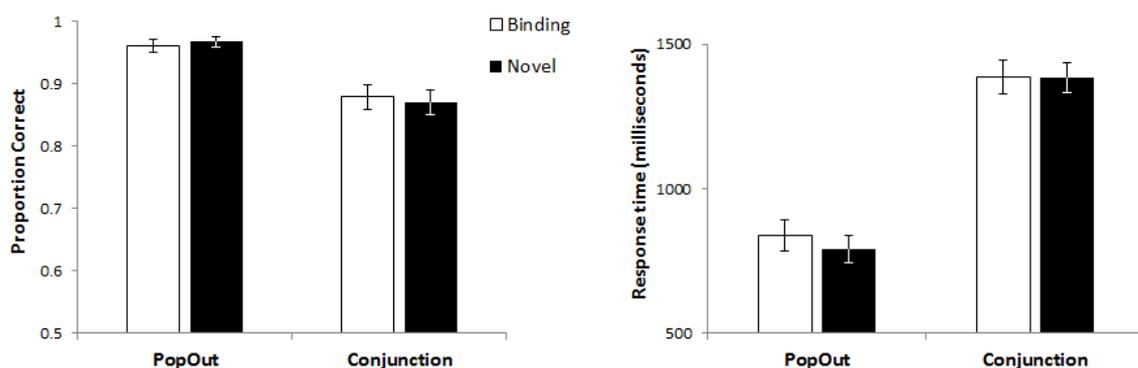


Figure 4.2. Mean proportion correct and response times in the two types of visual search tasks for both novel and binding change detection tasks. Error bars show standard errors of the mean.

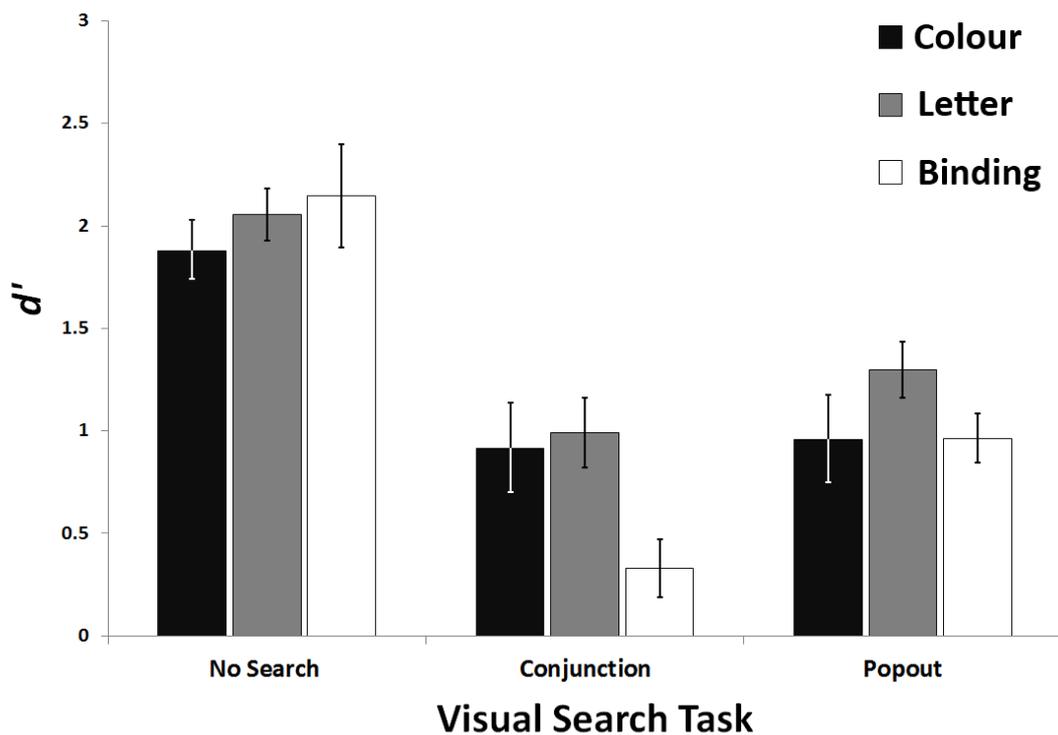


Figure 4.3. Mean  $d'$  values for the three change-detection conditions across the different visual search tasks presented in the delay period. Error bars show standard errors of the means.

### 4.3.3. Dual-task correlations

If it is the case that perceptual binding is the process driving the observed binding deficit, it might be the case that participants who have difficulty performing the conjunction search should be more likely to do poorly in the binding condition when a conjunction search task is presented in the delay period. To test this hypothesis, response times for each subject in the conjunction visual search conditions were correlated with their  $d'$  scores in the binding change-detection task/conjunction visual search task condition. The results showed a strong negative correlation ( $r = -.624, p=.006$ ). Importantly, this negative correlation was not present for novel letter ( $r = .164, p=.517$ ) and novel colour ( $r = -0.159, p=.529$ ) conditions, showing that it is not the case that performance in the conjunction visual search tasks was negatively correlated with accuracy in all change-detection tasks which included a conjunction visual

search task in the delay period. Furthermore, response times in the pop-out visual search tasks did not correlate with  $d'$  for any change-detection tasks with a pop-out visual search task in the delay period — see Figure 4.4 for all dual-task correlations.

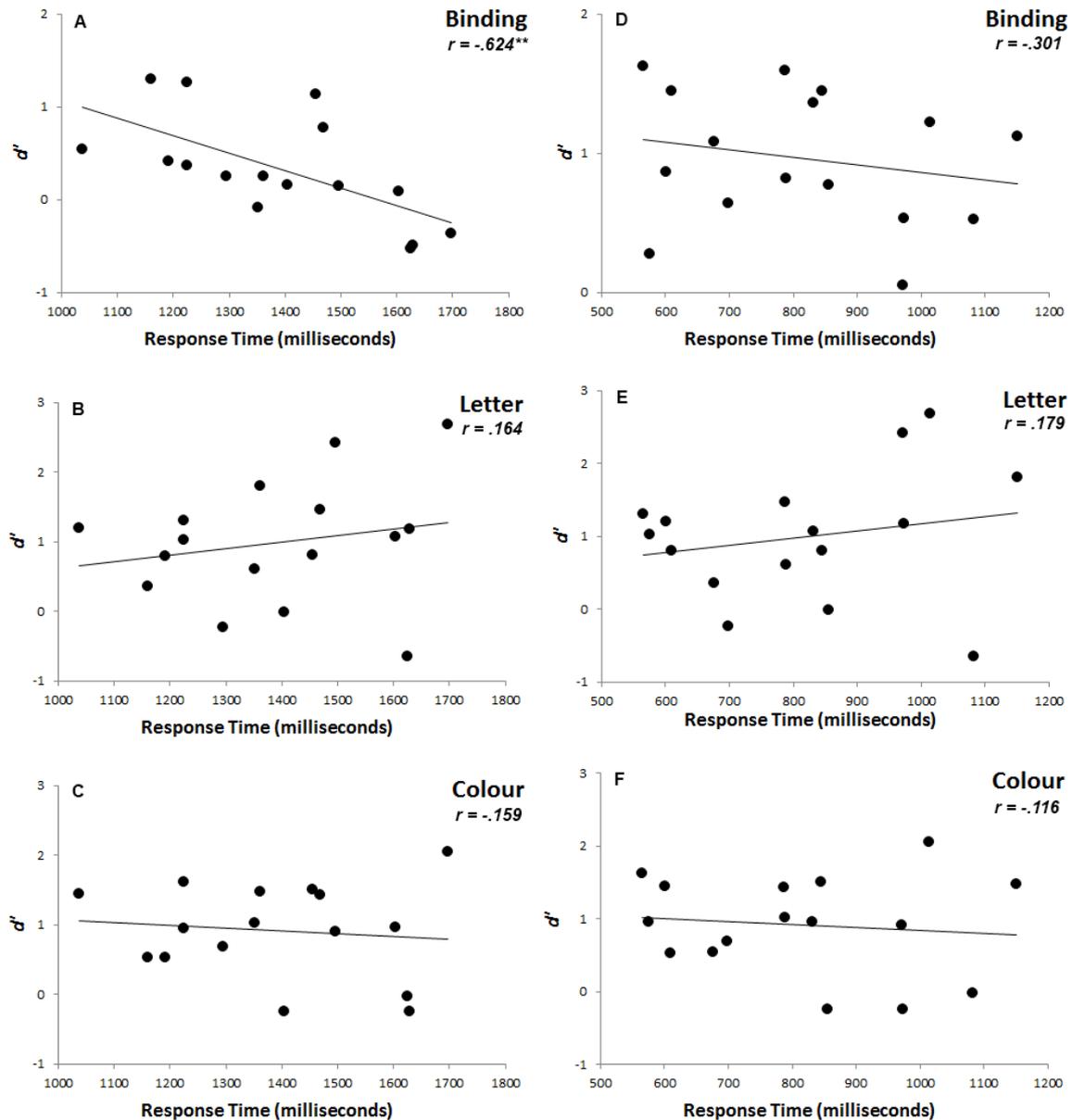


Figure 4.4. Correlations of response times in conjunction search trials (A-C) and pop-out search trials (D-F) with  $d'$  values in the different change-detection conditions.

In summary, it is clear that in the absence of a secondary visual search task, there is no difference between novel and binding changes when the test display is a single item, essentially replicating the findings of Wheeler and Treisman (2002). While a pop-out visual search task, which requires the simple detection of singleton visual features, affects change-detection performance, it does so equally for all change-detection tasks. A conjunction visual search task requiring binding of visual features, on the other hand, specifically disrupts binding in visual working memory as shown by both the poor performance in the conjunction visual search task/binding change-detection condition and the negative correlation between response times in the conjunction visual search task and  $d'$  scores in the visual search task/binding change-detection condition.

#### **4.4. General Discussion**

A range of seemingly disparate experimental manipulations of change-detection tasks have shown that, in certain situations, binding information is lost more readily from visual working memory than visual feature representations. These include the use of multi-item test displays (Wheeler and Treisman, 2002), the sequential presentation of items in the initial display (Allen et al. 2006) and the presentation of a multiple-object tracking task in the delay period. One cognitive process common to all these manipulations is perceptual binding, and the current study tested whether this was the process that causes the disruption of binding in working memory. To this end, two forms of a visual search task were presented in the delay period of a change-detection task, of which only one required perceptual binding. If perceptual binding is the critical process that disrupts binding in visual working memory, I hypothesised that this conjunction visual search task should reduce change-detection performance more for a binding condition than visual feature conditions (novel colour and letter conditions). A pop-out visual search task, on the other hand, should not specifically

disrupt performance in binding conditions, as the task does not require perceptual binding. This is precisely what the results showed, suggesting that perceptual binding and binding in working memory draw on common resources.

This result is important for two reasons. First, it adds weight to the feature-channel hypothesis (Wheeler & Treisman, 2002) in the long standing debate regarding the nature of visual working memory representations, which posits that visual features are maintained in separate stores or channels, with additional representations maintaining the associations between visual features. The strong object hypothesis (Luck and Vogel, 1997), on the other hand, is unable to account for binding information being lost more readily than visual features. Second, it sheds light on the interactions between perception and working memory that disrupt binding information in working memory more so than visual feature information. Namely, the current results highlight perceptual binding as a candidate process responsible for disrupting binding in visual working memory. This interpretation allows for a unitary framework that is able explain a range of experimental findings showing a binding deficit in change-detection tasks (Allen et al., 2006; Fougne & Marois, 2009; Wheeler & Treisman, 2002)

There are, however, a number of potential criticisms of this interpretation, which require close examination. First, a simpler explanation of why the conjunction visual search task disrupted binding information more than the pop-out version could be due to task difficulty. According to this account, it is not perceptual binding *per se* that disrupts binding information in working memory, but the mere fact that one secondary task is more difficult than the other. It is important to note that this issue does not detract from the contribution that this experiment adds to the debate about whether binding information can be lost independently of visual feature information. That is, regardless of *how* the conjunction visual search task differentially disrupted performance in the binding version of the change-

detection task relative to the novel visual feature conditions, the fact that it did is strong evidence against object accounts of visual working memory representation.

The issue of task difficulty is, however, a potential problem for the interpretation that perceptual binding is the process that drives the loss of binding information in working memory. There are two reasons why task difficulty is unlikely to be the source of the effect. First, while the average response time — an index of task difficulty — was certainly longer in the conjunction visual search condition (~1390 ms) than the pop-out version of the task (~810 ms), it was similar to the average response time reported for the secondary visual search task presented by Johnson et al. (2008). In their task, a response time of approximately 1250-1300ms was reported when the set size for the change-detection task was four items, suggesting a comparable level of difficulty to the conjunction visual search task presented here. However, this visual search task (which required no visual feature binding) did not specifically disrupt binding in working memory; the interaction between dual-task load (*search* versus *no-search*) and memory condition (*binding* versus *visual features*) did not come close to approaching significance ( $F < 1$ ).

In addition, the dual-task correlations reported here do not support the notion that task difficulty was the driving force behind the differential effects of the two visual search tasks. If the likelihood of successfully detecting a change (or correctly rejecting a non-change) is modulated by the difficulty of the search task presented, one would expect to observe a negative correlation between response times and  $d'$  values across all combinations of search task type and change-detection condition. That is, if the difficulty of the search task is driving performance in the change-detection task, participants who took longer to locate the odd-pair out in the search task should produce lower  $d'$  values regardless of the nature of the visual search task. This was not the case, however, with only the response times in conjunction search task modulating change-detection performance. Furthermore, this relationship between

conjunction visual search task response times and change-detection performance was only apparent for the binding condition. Taken together, the dual-task correlation results are not compatible with explanations that attribute the current set of results to differences in task difficulty between the conjunction and pop-out versions of the search task.

Another issue requiring closer examination is whether the conjunction visual search task described here does, in fact, require visual feature binding. An anonymous reviewer of a manuscript containing the current experiment suggested that the task could be performed successfully without the need to bind visual features. Specifically, it was suggested that the conjunction search task could be performed by filtering out a certain colour (e.g. the blue letters in [Figure 4.1](#)) and then selecting the non-matching letter from the remaining set (the letter G). According to this proposal, employing this filtering strategy essentially converts the task into a pop-out search task (“Where is the odd letter out?”). There are two objections to this idea. First, it is clear from the visual search results (both response time and accuracy measures) that the conjunction visual search task was certainly more difficult than the pop-out version of the task, suggesting that the two tasks recruited different cognitive processes. The second objection is an *a priori* argument against the notion that this strategy does not require perceptual binding. That is, by first selecting a set of items based on *colour*, and then selecting a specific item in that set based on *identity* information, one is effectively binding visual features. The very act of initially selecting a set of items based on a certain colour, followed by a single item from that set according to identity ensures that any subsequent decision is not being made based on a single visual feature dimension, but on a very specific colour-letter combination. This is the hallmark of conjunction visual search tasks, and it is impossible to perform the conjunction search task reported here without making comparisons between the items based on colour-letter combinations, as opposed to single visual feature dimensions (as is the case in the pop-out search task).

The major finding of the current study — that only conjunction visual search tasks disrupt binding in working memory — allows for the discounting of hypotheses that propose binding information to be especially susceptible to interference from *any* subsequent visual processing. This general interference hypothesis proposes that binding information is automatically maintained in visual working memory (i.e. it does not require additional attentional resources), but is more fragile than visual feature representations. According to this proposal, it is this relative fragility of binding information that causes it to be preferentially lost in whole-display change detection tasks (and not in single display change-detection tasks), due to the additional interference associated with the perceptual processing of a multi-item test display. The reason that the current study is evidence against this account is due to the pop-out search task disrupting binding and visual features information to a comparable degree.

While the current study is well positioned to discard the general interference hypothesis, it is ultimately unable to distinguish between an attentional account and a very particular version of interference account. That is, it is unable to determine if binding in working memory fails during the conjunction visual search task because attention, which is required for the maintenance of binding information in working memory, is diverted away from working memory representations to perceptual processes associated with the binding of visual features (the attentional account), or if binding in visual working memory is mandatory and automatic (i.e. does not require attention) but is particularly susceptible to interference from the attentionally mediated process of perceptual binding (the binding interference account). Although the current study does not speak to this impasse, there are compelling reasons, based on the extant literature on the topic, to favour the binding interference account. Specifically, a range of attentionally demanding secondary tasks presented during the delay period of change-detection tasks have failed to produce greater deficits in detecting binding

changes relative to novel visual feature changes (Allen et al., 2006; J. S. Johnson et al., 2008; Yeh et al., 2005). In addition, cueing a specific item in visual working memory (i.e. withdrawing attention away from the other items maintained in visual working memory) does not result in the “unbinding” of the uncued items’ visual features (Gajewski & Brockmole, 2006).

In conclusion, the current experiment provides further evidence for the feature-channel hypothesis (and against the object hypothesis), by showing that the maintenance of objects in working memory involves a representational system in which the associations between visual features is more susceptible to interference than the visual features themselves. Furthermore, this interference is not caused by the mere processing of any subsequent visual processing (even if it involves stimuli that contain the same visual feature dimensions as those maintained in working memory), but by the very specific process of perceptual binding. Finally, this finding is compatible with neuroscience models of visual working memory, which stress the largely overlapping, common neural substrates recruited by visual working memory and visual perception.

## Chapter 5: General Discussion

### 5.1. Summary

The experiments reported in this thesis have investigated, in a number of different ways, the nature of representations maintained in visual working memory. Each experiment provided evidence for a model of visual working memory that makes a distinction between visual feature representations and representations that code for the associations between visual features.

In *Study 1*, a change-detection task was used that included manipulations to address methodological concerns with previous studies. First, strategies that took advantage of feature-location binding — a possibility in the studies reported by Wheeler and Treisman (2002) and Johnson et al. (2008) — were nullified by ensuring that none of the locations occupied in the initial display were used again in the test display. Second, a retro-cue was presented in the delay period to assess the degree of feature binding in working memory prior to the interference produced by a multi-item test display. This question has been investigated previously by using a single item in the test display (e.g. Allen et al., 2006; Wheeler & Treisman, 2002), but this manipulation suffers from confounding strategies available to participants that make it difficult to interpret the results.

The pattern of results reported in *Study 1* allowed for two conclusions. First, when an item is cued in visual working memory — whether it be via a location cue or a feature cue — participants are able to detect binding changes at levels that are comparable to novel feature changes. This suggests that binding information is encoded and consolidated into working memory to the same extent as visual feature information. Second, when no item is cued in

working memory, a binding deficit occurs; that is, the detection of binding changes is made significantly more difficult than the detection of novel visual feature changes. This finding suggests that while binding information is successfully encoded and consolidated into working memory, it is more likely to be lost from working memory than are visual feature representations.

*Study 2* used a novel 2AFC paradigm to investigate the degree of competition between the target and lure in binding and novel feature conditions. In binding conditions, the lure contained a shape and colour from the initial display, but in a combination that did not match any items in the initial display. In the novel feature conditions, the lure contained either a colour or shape that was not present in the initial display. Participants made their selections by moving a mouse cursor to one of the items, and the degree of competition between target and lure was indexed by recording the  $x$  and  $y$  coordinates of the mouse cursor movements. Participants moved the mouse cursor in the direction of the lure more often in the binding condition than in the novel feature conditions, resulting in more curved trajectories in the binding condition. In addition, mouse trajectories in the binding condition changed direction between target and lure more often than in novel feature conditions. These findings are suggestive of a feature-based representational format as target-lure competition is more easily resolved when the lure contains novel visual features relative to conditions in which the lure contains novel feature combinations.

While *Study 1* provided evidence for the differential maintenance of visual features and binding information, it does not speak to the underlying mechanism by which multi-item test displays preferentially disrupt binding information in visual working memory. I hypothesised that multi-item test displays disrupt binding in visual working memory because the

perception of these displays requires extensive binding of visual features. If the binding of features in working memory recruits the same neural and information-processing operations that are used to bind visual features during perception, then multi-item test displays will necessarily disrupt binding information more than single-item test displays do. This disruption of binding information would, however, leave memory for visual features intact, leading to better performance in novel feature conditions relative to binding conditions.

To test whether perceptual binding and binding in working memory share a common underlying process, a dual-task procedure was used that required participants to perform a visual search task in the delay period of a change-detection task. One version of the search task required the binding of visual features (*conjunction search*), while a second involved the search for pop-out visual features (*pop-out search*). A single item was used as the test display. When no visual search task was presented in the delay period, there was no difference between binding and novel feature conditions. While the pop-out search task lowered performance in all change-detection conditions, it did so equally across these conditions. In contrast, the conjunction visual search task specifically impaired participants' sensitivity to binding changes relative to novel feature conditions.

## **5.2. The stage of failure underlying the binding deficit**

The interpretation proposed in this thesis is that the binding deficit observed in these studies is indicative of a failure to maintain binding information in working memory. That is, the stage of processing at which representation failure occurs is at the stage of working memory maintenance. Others have suggested that the binding deficit may be a result of a failure at the stage of comparing working memory representations to the items presented in the test display. According to this view, irrespective of the nature of visual working memory

representations, it is inherently more difficult to make comparisons based on visual feature associations than it is for visual features themselves (Delvenne et al., 2010). While comparing feature bindings requires the comparison of four visual features (e.g. a colour and shape in working memory and a colour and shape in the test display), visual feature changes only require the comparison of two visual features. As such, it “may not be entirely sensible” to directly compare memory for features and memory for feature bindings using change-detection tasks (Delvenne et al., 2010, p. 115).

The design of *Study 3* is well suited to address the claim that visual working memory maintains integrated object representations, with the locus of the binding deficit being the comparison stage of the change-detection task. In this study, the secondary task targeted the maintenance process directly, while keeping the comparison process constant across all levels of the secondary task factor. While the no-search and pop-out search secondary tasks did not produce a binding deficit, this effect was observed when a conjunction search task was performed. This binding deficit cannot be attributed to a difference in the comparison process for novel feature and binding conditions, as the comparison phase was the same regardless of the secondary task presented. In addition, the binding deficit is not restricted to tasks that require a comparison between a test display and visual working memory representations. Directly probing items in working memory has shown that visual features fail independently of each other (Bays et al., 2011; Fougner et al., 2010), and that binding information fails independently of working memory for visual features (Corballis et al., 2007). This is not to say that the comparison process is not more difficult in binding conditions compared to novel feature conditions. The account supported here is simply that any difference in difficulty at the comparison stage follows directly from a particular representational format of working memory maintenance.

### **5.3. A neural-cognitive “indexing” model of visual working memory representation**

Central to the model supported here is that visual working memory maintains two basic forms of representations: visual feature representations and separate binding representations coding the associations between visual features. This proposal is supported by behavioural findings from a range of experimental paradigms including change-detection tasks (e.g. Wheeler & Treisman, 2002), multiple-object tracking tasks (e.g. Alvarez & Thompson, 2009), rapid serial visual presentation (Corballis et al., 2007) and mixture modelling paradigms that independently probe different visual feature dimensions in working memory (e.g. Bays et al., 2011). In this section, I propose a neural-cognitive model capable of maintaining these two forms of working memory representations. In addition, this model is able to explain why (under certain conditions) binding representations are more prone to interference than visual feature representations.

The model is borne out of three claims, each of which is supported by an ever-growing body of research. First, visual feature dimensions are maintained in working memory in a modular fashion by the brain. For example, the maintenance of colour information recruits neural resources distinct from the maintenance of orientation information. Second, maintaining binding information requires neural resources distinct from those dedicated to the maintenance of visual features. Finally, the representation of visual features and binding information in working memory recruits the same neural workspace as that employed during visual perception.

### **5.3.1. Working memory feature-channels in the brain**

As mentioned earlier, Serences et al. (2009) have shown that the maintenance of colour or orientation information in working memory evokes distinct neural patterns for each visual feature dimension. This study employed MVPA to successfully predict which visual feature value was maintained in working memory based on the distributed pattern of activity across voxels in early visual areas. More traditional analyses also point to feature-based specialisation. Morgan et al. (2009) have integrated fMRI (using the traditional general linear model approach) and event-related potential data to show that orientation and colour are maintained by different neural circuits. The hypothesis that lower-level visual features are stored independently is also supported by behavioural findings that show different visual features decay from working memory at different rates (Magnussen, 2000). For example, orientation information is lost from memory much more rapidly than texture information (Pasternak & Greenlee, 2005).

This functional specialisation of visual working memory extends beyond lower-level features, to higher-order category classes. A number of studies have shown that maintaining faces and places recruit different neural regions (Ranganath et al., 2004; Ranganath & D'Esposito, 2005; Ranganath, 2006). Specifically, while maintaining faces causes sustained activation of the fusiform face area, maintaining houses in working memory is instantiated by sustained BOLD responses in the parahippocampal place area.

### **5.3.2. Working memory feature bindings in the brain**

A critical region in visual working memory maintenance is the posterior parietal area, especially the intraparietal sulcus (Kawasaki et al., 2008; Mitchell & Cusack, 2008; Todd & Marois, 2004; Xu & Chun, 2005; Xu, 2007). A common finding is that this brain region is

modulated by the number of items maintained in working memory. Importantly, this set-size modulation occurs for a range of different stimuli. For example, Todd and Marois (2004) used coloured circles as stimuli while Xu and Chun (2006) used simple and complex shapes. Kawasaki et al. (2008) showed that posterior parietal regions were responsive to set-size increases for shape, colour and motion information. A common interpretation of these studies is that the intraparietal sulcus is responsible for maintaining integrated object representations in working memory (e.g. Xu, 2007) i.e. it is a neural region able to maintain a range of visual feature dimensions.

Another possibility is that this region maintains spatial “pointers” (in the language of Pylyshyn, 2001) that index the visual features present at a number of locations (Mitchell & Cusack, 2008). According to the model proposed here, these indexes serve the function of individuating objects in working memory and binding visual features. Importantly, these indexes do not store any visual feature representations themselves. They merely “point to” visual features represented elsewhere in the brain. It is no surprise then that the BOLD response in posterior parietal regions track with set-size for a wide range of visual features. This does not occur because these regions are “storing” different visual features, but because the IPS is exhibiting increased signal in response to an increase in the number of pointers or indexes being maintained in working memory.

The fMRI findings discussed so far cannot distinguish between a storage account of intraparietal sulcus activity and an account that designates an indexing role to this region: both accounts predict that activity should increase as set size increases regardless of the visual features presented in the initial display. There is compelling evidence from other studies that are supportive of an indexing account, however. First, Morgan et al. (2011), have shown (using MEG) that gamma oscillatory activity emanating from parietal areas was greater for a conjunction WM task requiring maintenance of bound information (orientation

and colour) than for tasks requiring maintenance of only colour or orientation information. More importantly, however, they found that this gamma activity was correlated with accuracy performance in the conjunction condition but not in the single visual feature conditions. If parietal regions are involved in the storage of visual features, then activity in these regions should have correlated with performance in the visual feature conditions. In addition, the functional role of posterior parietal regions was assessed directly by the same research group using TMS (Morgan, Jackson, Van Koningsbruggen, Shapiro, & Linden, 2012). In this study, the authors found that applying a TMS burst to posterior parietal regions specifically disrupted performance in binding conditions relative to single feature conditions. Again, if posterior parietal regions are directly involved in maintaining visual features, TMS should also have disrupted working memory in the single feature conditions.

### **5.3.3. A common neural workspace between working memory and visual perception**

The final aspect to the model proposed here is that the feature dimension specificity of ventral brain regions, and the binding specialisation of posterior parietal regions mirror the functional specialisation observed in visual perception. For example, the regions that show working memory specialisation for faces and places (e.g. Ranganath & D'Esposito, 2005) are also the regions involved in the perception of these stimuli classes (Epstein & Kanwisher, 1998; Kanwisher, McDermott, & Chun, 1997). More direct evidence comes from the study of Serences and colleagues (2009). In addition to finding that distinct patterns of activity underlie working memory for orientation and colour information, the authors found that training their classifier using a perception task was also able to distinguish the contents of working memory.

A striking example of a neural mechanism common to visual perception and visual working memory comes from Kang, Wook Hong, Blake, and Woodman (2011), who have

shown that the contents of visual working memory can directly influence conscious visual experience. Their study was modelled on a robust perceptual phenomenon called *motion repulsion*, in which the perceived angular separation of two moving stimuli is greater than the actual angular separation. This misperception can be strikingly large, deviating by up to 20° when the actual angular separation is approximately 30° (Hiris & Blake, 1996). The participants in the study of Kang et al. (2011) were required to estimate the direction of movement of a set of dots, while they maintained the direction of another set of dots in visual working memory. The authors found a motion repulsion effect, with the estimates tending away from the direction of the direction maintained in working memory. The authors were able to rule out a range of alternative explanations including eye movements, visual priming and visual aftereffects. This study is strong evidence for a neural resource common to both visual perception and working memory.

This pattern of results is not limited to the representation of visual features. As discussed earlier, there is substantial evidence that posterior parietal regions play a role in the maintenance of binding information in working memory. Similarly, the IPS is preferentially recruited by conjunction visual searches relative to pop-out search tasks (e.g. Wei et al., 2011). Multiple-object tracking tasks, which require the binding of location and identity (e.g. Botterill, Allen, & McGeorge, 2011) also recruit posterior parietal regions (Jovicich et al., 2001). The proximity of neural regions recruited by these different tasks is illustrated in [Figure 5.1](#). Taken together, these findings are highly suggestive of a binding system instantiated by posterior parietal regions, which operates across the domains of visual perception and working memory maintenance.

#### **5.3.4. Interpreting thesis data in light of this model**

An appealing aspect of the model described here is that it is well equipped to explain the experimental findings of the current thesis. Because visual features and feature-bindings are proposed to be represented in different neural regions, the model allows for binding information to be lost independently of visual feature representations. It is also able to explain why binding information in working memory is lost under certain experimental manipulations of the change-detection task. These include the presentation of multi-item test displays tasks (*Study 1*), conjunction visual search tasks in the delay period (*Study 3*) and multiple-object tracking tasks in the delay period (Fougnie & Marois, 2009). In each case, these manipulations require extensive perceptual binding, and the model proposed here is that this process recruits the same neural resource required to maintain binding in visual working memory (see Figure 5.1).

In addition, this model is also compatible with behavioural findings that have been interpreted as evidence for an object-based account of visual working memory. The object-based benefit (Fougnie et al., 2012; Olson & Jiang, 2002; Xu, 2002) shows that maintaining  $x$  visual features across  $\frac{x}{2}$  objects (conjunction conditions) is easier than maintaining  $x$  features across  $x$  objects (disjunction conditions) — see Figure 1.3. That is, performance in these tasks is modulated by the number of objects, not the number of visual features. This is not surprising, however, as the number of indexes that need to be maintained by posterior parietal regions is doubled in the in the disjunction condition relative to the conjunction condition.

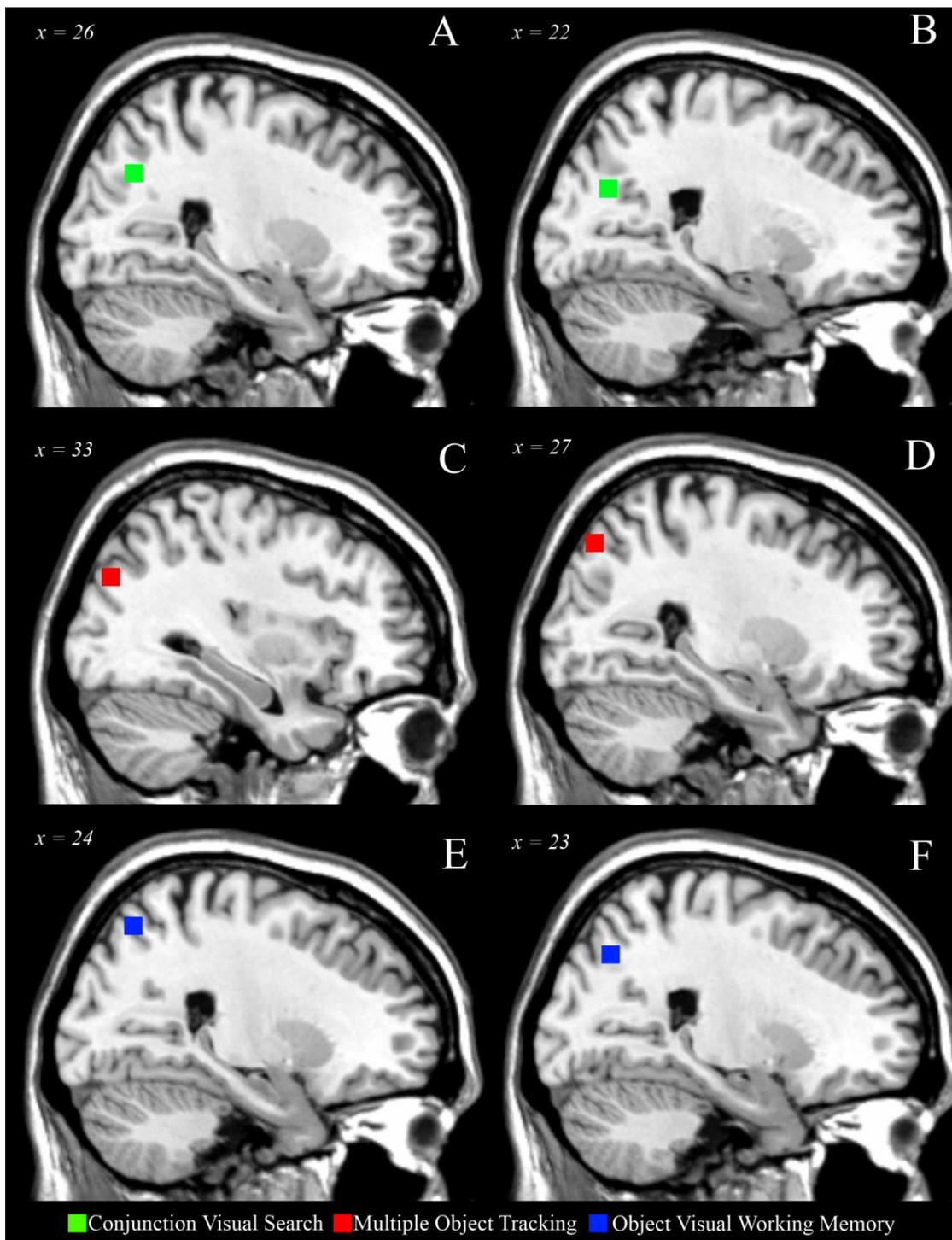


Figure 5.1. Peak activations in posterior parietal regions for a number of studies across three different cognitive tasks. A: Conjunction Search > Feature Search (Wei et al., 2011); B: Conjunction search > Feature Search when matched for difficulty (Donner et al., 2002); C: Multiple Object Tracking > Passive Viewing (Jahn et al., 2012); D: Multiple Object Tracking > Passive Viewing (Jovicich et al., 2001); E: Region modulated by load in visual working memory task requiring colour-location binding (Todd & Marois, 2004); F: Region showing load sensitivity to task requiring the maintenance of shape, colour and motion direction (Kawasaki et al., 2008). Peak activations are shown on a standard MNI brain. For those studies reporting Talairach coordinates, coordinates were transformed to MNI space. Studies cited in the text but not shown here used an individual subject region of interest approach (i.e. no coordinates were reported).

#### **5.4. Limitations of the current thesis**

The major limitation of the current thesis is that studies 1 and 3 used letters as stimuli, which may have recruited verbal working memory processes in these tasks. While verbal recoding was discouraged with the use of articulatory suppression, it is not clear if a verbal load of two digits is sufficient to eliminate entirely the use of verbal working memory to aid performance. Vogel, Woodman, and Luck (2001) have shown that including a verbal load of two items is able to reduce performance from ~95% correct to ~75% correct in a change-detection task using four letters as memory stimuli. This verbal load performance was similar to conditions in which the memory items were coloured squares. The problem, of course, is that colours are also nameable visual properties, so while a verbal memory load may have reduced its contribution, residual verbal working memory resources may have still aided performance in both the colour and letter conditions.

Morey and Cowan (2004) have suggested that a verbal load of two items is not sufficient to isolate visual working memory processes. They have shown that this verbal load produces equivalent performance to a control “no load” condition when the memory display is four coloured squares. It is only when the verbal load was seven items did performance drop significantly.

I cannot discount the possibility that verbal working memory processes may have contributed to the current set of results, although this criticism is not one specific to these experiments. While other studies may not use letters, they do use nameable stimuli (e.g. colours and common shapes). One way of getting around the use of verbal working memory could be to use novel stimuli which do not have semantic representations associated with them. This was employed in *Study 2*, which used Rune-like characters (see [Figure 3.1](#))

## **5.5. General Conclusion**

A Scopus database search<sup>19</sup> shows that, in the five years after the publication of the hallmark paper by Luck and Vogel (1997), 27 articles were published related to binding in visual working memory. In the five years prior to the submission of this thesis, that number had climbed to 128. Much of this intense research can be divided into two theoretical camps: those proposing that visual working memory maintains integrated object representations (e.g. Luck & Vogel, 1997), and those proposing a feature-based representational format (e.g. Wheeler & Treisman, 2002).

The results of the current experiments are overwhelmingly in favour of the feature-based account. Indeed, the model of visual working memory representations proposed here is very similar to that proposed originally by Wheeler and Treisman (2002). It makes a distinction between visual feature representations and feature-binding representations. The difference between the model proposed here and that of Wheeler and Treisman (2002), is that I do not propose binding in working memory to be specially contingent on sustained general attention. Instead, I propose that binding fails in working memory when operations specific to binding visual features are employed in subsequent visual processing. This distinction is a subtle one: I argue that the binding deficit occurs because a single binding *process* is shared by both visual perception and visual working memory, causing a conflict when binding information needs to be maintained in working memory in addition to the binding of visual features in perception. This differs from the view of Wheeler and Treisman (2002), who propose a general attention *resource* is shared by perception and working memory.

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<sup>19</sup> Search term: (“visual working memory” OR visual short-term memory”) AND binding

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