Individual differences in visual perception capacity and related brain morphology

Joshua. O. Eayrs

Institute of Cognitive Neuroscience

University College London

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I, Joshua Owen Eayrs, confirm that the work presented in this thesis is my own. Where information has been derived from other sources I confirm that this has been indicated in the thesis.

The experiments presented in chapters two and three of this thesis are currently under review for publication in *Journal of Experimental Psychology: Human Perception and Performance* with my supervisor, Nilli Lavie, as co-author.

Abstract

Limited capacity for perception results in various phenomena of inattentional blindness in task conditions that load perceptual capacity. These effects have been extensively studied under the load theory framework, with numerous demonstrations spanning a wide variety of perceptual load manipulations. Research also established contrasting effects of loading perception versus cognitive control functions (e.g. working memory). The convergence of findings across different manipulations of perceptual load together with the contrasting effects of cognitive control load suggests a generalised capacity for perception, which is distinct from general cognitive capacity. The purpose of this thesis was to examine this hypothesis further, using an individual differences approach and relating traditional visual perception and awareness paradigms to the phenomenon of subitizing: the ability to detect a limited number of items in parallel from a brief exposure that has traditionally been studied within the enumeration literature.

The research first extended perceptual load effects to measures of unattended processing in an enumeration paradigm, demonstrating that distractor effects are only found within subitizing capacity but not in set sizes that exceed capacity (Chapter 2). A series of individual differences experiments then revealed significant correlations between tasks involving subitizing, motion tracking, ‘change blindness’ and ‘inattentional blindness’. These relationships were furthermore established to withstand controls for non-perceptual factors, establishing perceptual capacity as distinct from working memory capacity or general cognitive effort (Chapters 3-4). Finally, voxel-based morphometry analyses of structural brain images established distinct correlates of grey matter density for perceptual capacity across tasks (Chapter 5).

Taken together, the results of this thesis establish individual differences in perceptual capacity across a diverse range of paradigms and stimuli, demonstrating a common, general capacity limit for perception which correlates with individual differences in performance and grey-matter density and is independent from other cognitive constructs such as number estimation abilities and executive working memory.

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Chapter 1

General Introduction

1.1 Preface

We are never more appreciative of the limits to our attention than when we are faced with something apparently obvious to which we were entirely oblivious. Be it an oncoming vehicle we only just spotted in time or a friend we failed to notice despite looking directly at him, our environment presents any number of situations in which we can be reminded of our limitations. The consequences of these failures can range from slightly embarrassing to life threatening; and performance of many safety-critical roles in security, medicine and transport are dependent upon people's limited attentional abilities. It is therefore an important goal of research to characterize the limits of our attention which dictate our successes and failures. Accordingly, a great deal of research effort has been dedicated over recent decades to understanding which situational factors lead to failures of attention and awareness. However, considerably less research has focused upon the attributes which determine whether a given individual is more or less susceptible to these failures. An individual differences approach to this question will both inform theories of attention in general and potentially provide a means of reducing risk by identifying individuals who are better able to perform in attention-demanding roles.

Previous research has provided considerable evidence that limitations on attentional processing can be described in terms of limited perceptual processing capacity, which underlies performance and awareness across varied perceptual task demands (e.g. Lavie, 1995; 2010; Lavie, Hirst, DeFockert & Viding, 2004). The primary aim of this thesis was therefore to investigate the construct of a task-general perceptual capacity limitation in order to understand how individuals might differ in terms of their attentional abilities. I used an individual differences approach in order to better understand the manifestations of perceptual capacity both in diverse behavioural effects and in brain structure. To this end I employed classic 'inattentional blindness' paradigms, which have been extensively established as demonstrations of the limited capacity for attention and awareness. I also used an object tracking task, which involves sustained perceptual demands over an extended period, to further establish the generality of the underlying capacity limitations. In conjunction with these paradigms I focused on the ‘subitizing’ phenomenon from visual enumeration literature; wherein the observer is able to efficiently report only a limited number of stimuli from brief presentations. In combining these paradigms I sought to investigate the nature of shared attentional limitations across all manner of perceptual demands. In order to relate the subitizing phenomenon to the existing load theory literature I first investigated distractor processing in a visual enumeration task. Following this I investigated common variance underlying perceptual processing in the aforementioned tasks while also establishing this as a distinct capacity from non-perceptual cognitive abilities by controlling for working memory capacity. Finally I used structural brain imaging to investigate the correlates of perceptual and cognitive capacities in regional grey matter density of the brain.

In section 1.2 of this chapter I will present the load theory of attention as a framework for understanding attentional limits and discuss literature regarding perceptual and cognitive limitations on attention. In section 1.3 I will present parallel evidence for attentional capacity limits shared across a range of paradigms, focusing upon subitizing. Finally, in section 1.4 I will discuss evidence for attentional capacity limits in the brain and individual differences in brain structure.

1.2 Load theory

As stated in the Preface, the aim of this thesis was to characterize perceptual processing limitations which underlie failures of awareness resulting from diverse task demands. The load theory of attention and cognitive control (Lavie, 1995; Lavie et al. 2004) provides a powerful framework for understanding processing limitations in attention-demanding tasks.

Load theory research has established convergent effects of numerous sources of ‘perceptual load’, suggesting a common underlying resource for perceptual processing. Thus, in the following section I will review literature regarding the load theory of attention, focusing in particular on the effects of different sources of load on task performance.

Failures of attention can take two basic forms: when engaged in a task, people can fail to notice stimuli even if they are salient, task-related and actively being searched for. On the other hand, people might be unable to avoid distraction by entirely irrelevant stimuli, even if they’re trying to ignore them. This contradiction is resolved in the load theory of attention which describes a limited perceptual capacity for the representation of task-relevant information. When people are performing a task with relatively low perceptual load there is spare capacity available, which automatically ‘spills over’ to other stimuli – leading to distraction. When performing a task of higher load (involving a greater number of stimuli or more complex stimulus discriminations) capacity is more likely to be exhausted, eliminating spill-over to distractors.

The initial formulation of load theory was based upon distractor interference paradigms, in which participants attempt to identify central target stimuli while ignoring simultaneously presented distractors. In this paradigm, distractors are found to significantly interfere with task performance if they share the identity of task relevant stimuli (Eriksen & Eriksen, 1974). For example in the Eriksen flanker task, participants search an array of letters for a pre-specified target letter (e.g. an X or an N; Figure 1.1); on a subset of trials, a distractor letter is presented in a separate location. The distractor letter can match either the presented target letter (compatible), the target letter that is not presented (incompatible) or a non-target letter (neutral). The typical result in experiments using this paradigm is that the presence of incompatible distractors results in significantly slower search times than compatible or neutral distractors. However, distractors do not need to share the identity of task-relevant stimuli to attract attention: Salient stimuli have been shown to significantly affect visual search even when their identity is entirely irrelevant to the task (e.g. Theeuwes, 1991; 1992; Forster & Lavie, 2008).

Lavie (1994; 1995) added an additional dimension to this paradigm by manipulating the perceptual load of the central target stimuli. In a low load condition, participants searched for targets presented alone or among homogeneous non-targets (e.g. an N presented among five O's; Figure 1.1) and in a high load condition the target was presented among heterogeneous non-target letters. The classic result of these experiments is that the distractor interference effect (i.e. the slower search times in the presence of incompatible distractors) is significantly reduced in the high load condition relative to low load. That is, target-incompatible distractors cause significantly slower search times in low load, but not in high load. This indicates that in the low load condition the task is not sufficiently demanding to exhaust perceptual capacity, which therefore spills over to the distractors. The increased number of potential target letters in the high load condition places more demands on perceptual processing as it becomes necessary to discriminate several individual letters; capacity is therefore exhausted and cannot spill over to the distractors. This result has been replicated with various modifications, including presentation of distractors at fixation (Beck & Lavie, 2005), socially salient categories of targets and distractors such as faces (Thoma & Lavie, 2013), distractors which are entirely irrelevant to the task (Forster & Lavie, 2008) and distractors presented in a separate sensory modality (Dalton & Lavie, 2004).

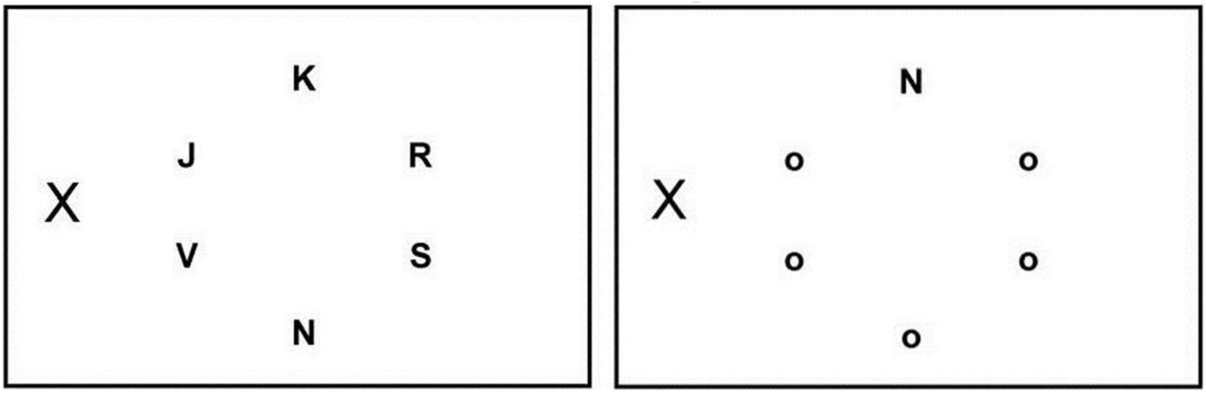

Figure 1.1 Example of the response competition flanker task demonstrating visual search for a target letter (N) among high (left) and low (right) load non-targets and an incongruent flanking distractor (X) to the left of the search array.

Thus, an increase in search-relevant set size is taken to increase the load on perceptual processing, exhausting capacity and eliminating distractor ‘spill-over’ to all manner of distractors. However, perceptual capacity is not only loaded by increased set size, but rather by the number or complexity of perceptual operations that must be performed to complete the task (Lavie & Torralbo, 2010). Numerous studies have established convergent effects when perceptual capacity is loaded by a variety of manipulations of perceptual complexity.

For example, in one manipulation of load, participants are presented with a rapid serial visual presentation (RSVP) of upright and inverted cross stimuli of various colours (Figure 1.2). In the low load condition, participants are instructed to respond to any red cross, regardless of orientation. In the high load condition they are instructed to respond only to upright yellow or inverted green crosses. The same effects are observed in this paradigm as in the letter search task as used in the original investigations (Schwartz et al. 2004; Carmel, Saker, Rees & Lavie, 2007; Carmel, Thorne, Rees & Lavie, 2011). In this paradigm the exact same stimuli are presented in high and low load conditions, the only difference being the number of features that are necessary to define the target stimulus. Thus, stimuli which require more perceptual resources to discriminate task-relevant stimuli from distractors produce results congruent with increased perceptual load.

Subsequent research has established load effects using various other manipulations of perceptual complexity. For example, identification of target objects which are presented either upright (low load) or inverted (high load) has been shown to affect subsequent distractor recognition (Lavie, Lin, Zokaei & Thoma, 2009) despite the exact same images being presented in both conditions. Distractor processing is also reduced when participants identify letter targets presented in non-word letter strings compared to their presentation in words of equal length (Brand-D'Abrescia & Lavie, 2007).

The effects of perceptual load in each of these paradigms (and more discussed in following sections) all converge upon the same conclusion: Increased perceptual load leads to reduced processing of task-irrelevant stimuli. The converging result across a diverse range of paradigms suggests a common underlying resource which can be exhausted by perceptually complex tasks.

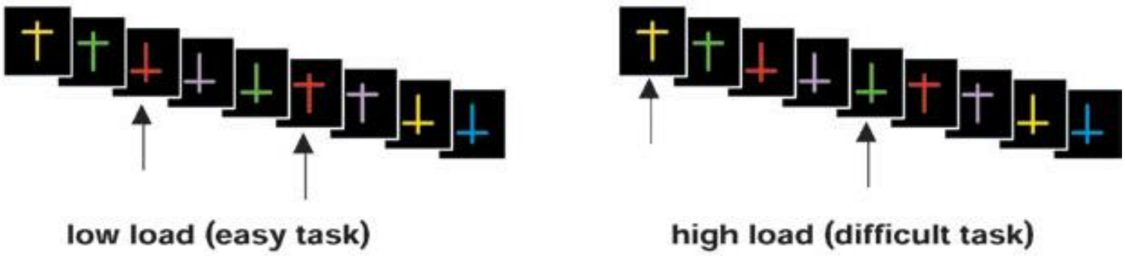

Figure 1.2 An RSVP task in which targets are defined by either a single colour (low load; left) or by a conjunction of colour and orientation (high load; right)

1.2.1 Load theory and visual detection

The level of perceptual load has therefore been established as a key determinant of the degree to which an irrelevant distractor will interfere with task performance. However, distractor interference and distractor-related brain activity are necessarily indirect measures of perception which do not lead to conclusions regarding subjective awareness. To address this issue it was necessary for further experiments to establish whether perceptual load affects the ability of a participant to consciously report the presence or absence of a stimulus, as in the 'inattentional blindness' paradigm.

Inattentional blindness refers to the observation that people will fail to notice even very salient and apparently obvious stimuli if their attention is occupied by a task (e.g. Neisser, 1979; Mack & Rock, 1998; Simons & Chabris, 1998). In a typical inattentional blindness paradigm the participant is engaged with a visual task such as judging the relative length of the arms of a cross (e.g. Figure 1.3). As they perform this task an unexpected 'critical' stimulus is presented at or near the attended location and the participant is subsequently asked if they noticed it. Awareness of the critical stimulus is reliably lower than on control trials where the participant is expecting (and looking for) the critical stimulus. Inattentional blindness occurs even when the critical stimulus is presented directly at fixation and when it is present for an extended period of time during tasks which require sustained attention (Most, Simons, Scholl & Chabris, 2000). Further research has also shown that the effects of inattentional blindness extend beyond the visual domain and into other sensory modalities (e.g. 'inattentional deafness': MacDonald & Lavie, 2011; Dalton & Fraenkel, 2012 and 'inattentional numbness': Murphy & Dalton, 2016).

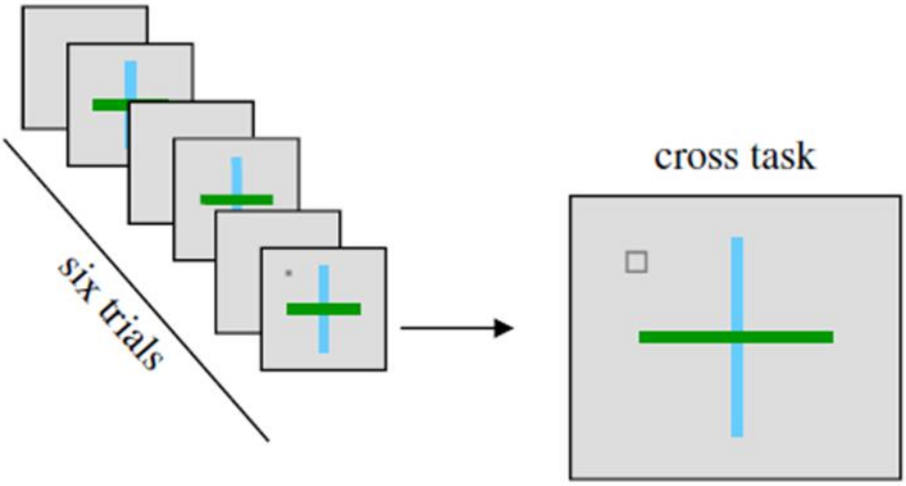

Figure 1.3 An example of the inattentional blindness cross arm length discrimination task as used commonly in inattentional blindness research, in this version a ‘low load’ condition involves discriminating arm colour rather than length (Cartwright-Finch & Lavie, 2007).

Inattentional blindness is not limited to entirely unexpected stimuli: More recent research has established that even if the participant is aware that a critical stimulus might appear and are actively looking for it, their ability to detect its presence is still severely limited (e.g. De Fockert & Bremner, 2011; Ward & Scholl, 2015). A related phenomenon is ‘change blindness’ (Rensink, O’Reagan & Clark, 1997) wherein people are told to actively search for some kind of change in a stimulus over a period of several seconds. Provided that there is some form of visual disruption such that the change does not ‘pop-out’, then it may go unnoticed for several seconds of effortful search. For example, when an image is presented on and off repeatedly with a blank interval such that the image appears to ‘flicker’, changes which appear in-between image presentations (flickers) are difficult to find (Figure 1.4). Once noticed however, the change seems obvious to the previously change-blind observer and they are easily able to find it on repeated presentations.

Rates of inattentional blindness and change blindness are increased in relatively more difficult tasks (involving greater perceptual demands) for example attending two categories of stimuli rather than one (Simons & Chabris, 1998), keeping track of faster moving stimuli (Simons & Jensen, 2009) or holding complex strings of digits in memory (Fougnie & Marois, 2007; although see De Fockert & Bremner, 2011 for contrary evidence, discussed later). As in inattentional blindness, increased attention demand leads to increased rates of change blindness. For example when the observer's attention is engaged in a secondary task at the same time they are less likely to notice the change (Beck, Rees, Frith & Lavie, 2001; McCarley et al. 2004).

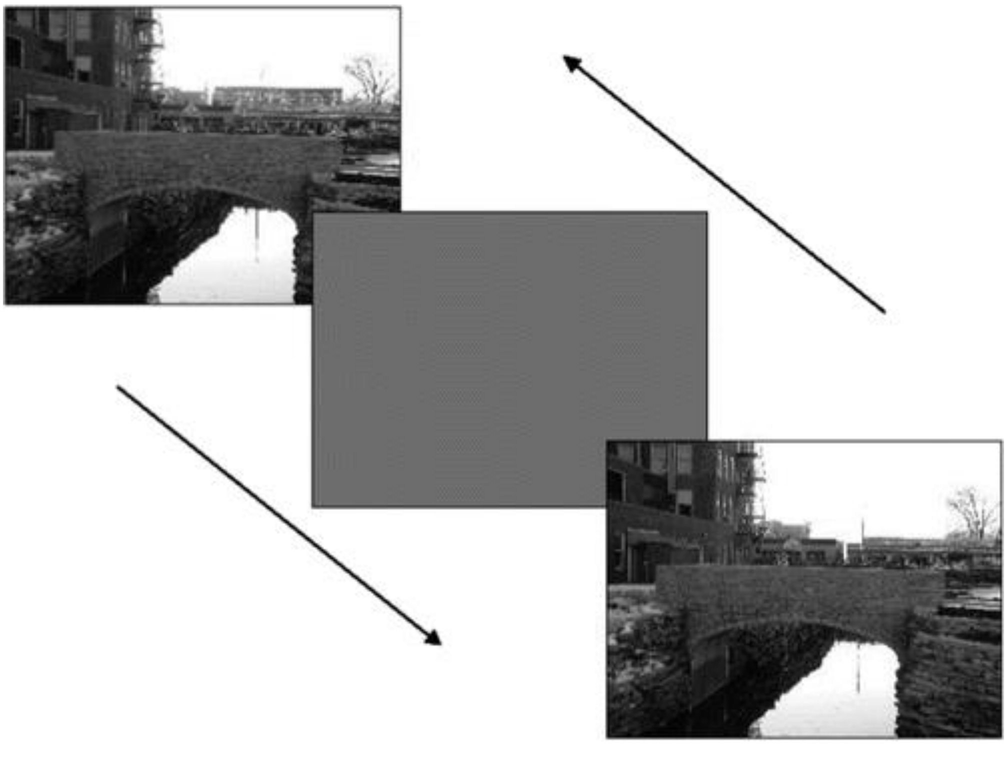

Figure 1.4 An example of the change blindness flicker task, the image is identical in each sequential presentation except for the removal of the rectangular building in the background (Simons & Ambinder, 2005).

Cartwright-Finch and Lavie (2007) applied load theory directly to the inattentional blindness 'cross' paradigm (Figure 1.3). In their high load condition participants performed the length discrimination task as described previously, whereas participants in the low load condition instead reported which of the lines was presented in a pre-specified colour. Rates of inattentional blindness were significantly higher among participants in the high load condition relative to those in the low load condition. Following experiments applied the typical load manipulation of a visual search with small (low load) or large (high load) set sizes (Figure 1.5) and established the same result: Increased load lead to decreased likelihood of the participant noticing the critical stimulus. This finding establishes perceptual load as a key determinant of inattentional blindness and provides insight to the earlier observation that inattentional blindness rates are affected by task difficulty.

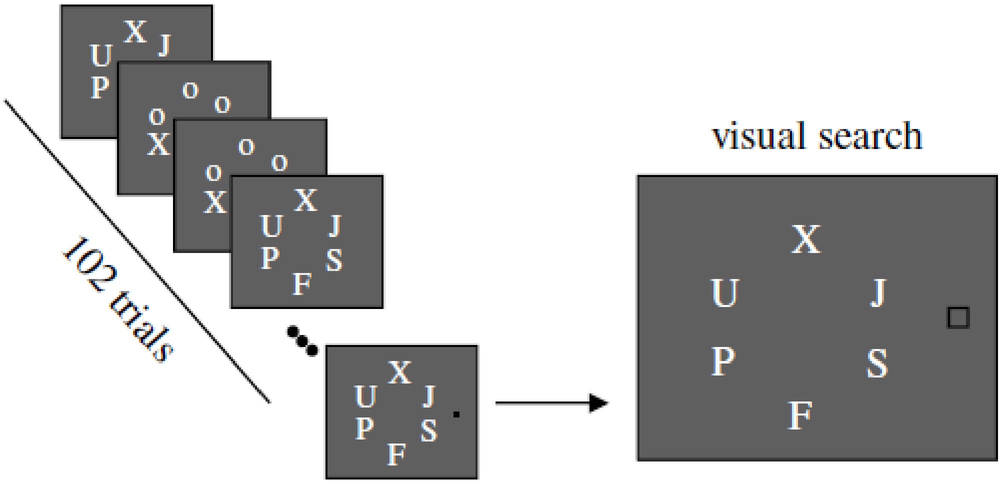

Figure 1.5 An example of the load induced blindness paradigm with a visual search manipulation of load as used by Macdonald & Lavie (2008).

This paradigm was subsequently developed further by Macdonald and Lavie (2008) to incorporate repeated presentations of the critical stimulus, a version termed ‘load-induced blindness’. Their participants performed the same letter search task as used in standard load theory distractor paradigms and as employed by Cartwright-Finch and Lavie (2007) in their second experiment. This time, the critical stimulus was presented on a random subset of trials and participants responded on each trial to indicate whether or not it had been present. As the critical stimulus is repeated in multiple trials in this paradigm the authors were able to measure participants’ detection sensitivity and response criterion as opposed to relying on the binary blind/ not blind comparison as in standard inattentional blindness paradigms. This also allowed the authors to measure stimulus detection in both high and low load conditions for each participant where the traditional paradigm necessitated separate samples. Detection sensitivity (d’) was significantly reduced in the high perceptual load condition relative to low perceptual load, with no significant change in response bias (β). Thus, even though they were actively attempting to detect the presence of the critical stimulus on each trial, participants were still less likely to notice it when faced with a search involving increased perceptual load. This effect applied both for relatively frequent and infrequent appearances of the critical stimulus (50% or 17% of trials respectively). This paradigm also allowed the authors to rule out an alternative explanation for the inattentional blindness phenomenon – ‘inattentional amnesia’ (Wolfe, 1999). It has been suggested that rather than failing to perceive the critical stimulus in a standard inattentional blindness paradigm, observers may perceive but then rapidly forget as it is not relevant to the task. Inattentional blindness, it was argued, could therefore be a post-perceptual phenomenon rather than an effect of perceptual limitations. This is difficult to rule out in traditional inattentional blindness paradigms, however in the load induced blindness paradigm it was possible for Macdonald and Lavie (2008) to include a condition in which participants responded to the critical stimulus immediately, before making any other task response. Their results replicated those of their other experiments: Even when the critical stimulus response was made before the search response, detection sensitivity was significantly reduced by increased search load. This further demonstrates that failures of awareness demonstrated by subjective blindness phenomena can be attributed to failures of perception rather than memory or other cognitive constructs (see also Ward & Scholl, 2015).

1.2.2 Cognitive control load

There is an important distinction in load theory between the effects of perceptual load and those of 'cognitive load' or load on cognitive resources which underlie non-perceptual processing (e.g. working memory). The distinction between cognitive and perceptual load is important as it further specifies those processes that do and do not contribute to failures of awareness. That is, manipulations of cognitive load do not involve increased perceptual complexity and do not therefore exhaust perceptual capacity. This distinction was demonstrated by De Fockert, Rees, Frith and Lavie (2001) who found that loading working memory can have the opposite effect to perceptual load. Specifically, participants were presented with a name classification task in which they reported whether a name presented on screen belonged to a famous politician or musician while ignoring compatible or incompatible distractor face images. While participants performed this task, they also held in memory a string of digits in either ascending order (e.g. 2 3 4 5 6 7 - low working memory load condition) or in random order (e.g. 7 4 3 6 2 5 – high working memory load). Participants were instructed to memorize these digits in order and then hold them in memory while performing a visual search task before finally reporting the memorized digits at the end of the trial (Figure 1.6). Distractor interference from the task-irrelevant face images was significantly increased in the high working memory load condition relative to low working memory load.

This finding was further explored by Lavie et al. (2004) who applied the same manipulation of working memory load to the traditional load theory paradigm (i.e. a letter search task with response competing distractor letters). Working memory load was associated with significantly increased search interference by the response competing flanker letters (Figure 1.5). That is, when participants held a more complex string of digits in memory they were more likely to involuntarily process distractor stimuli, as with task irrelevant distractor faces in the previous study. This was the case in both low and high perceptual load conditions, indicating that cognitive and perceptual load have independent and contrasting effects (Lavie et al. 2004; Experiment 3). This suggests that working memory load reduces the availability of top-down cognitive control resources used to determine task priorities. Under high perceptual load there is insufficient perceptual capacity to process all potentially relevant stimuli in parallel, so only those stimuli which have been prioritized by top-down control are processed. Under high working memory load, the resource that determines which stimuli to prioritize is unavailable and distractors once again receive attention.

Figure 1.6 An example of the cognitive load paradigm employed by De Fockert et al. (2001; left) and Lavie et al. (2004; right) with congruent or incongruent face (left) and letter (right) distractors.

Since these original demonstrations a great deal of research has reinforced the conclusion that perceptual and cognitive load typically have opposite effects on distractor processing (as well as critical stimulus detection in inattentional blindness; De Fockert & Bremner, 2011). Cognitive control load is predominantly manipulated using lexical maintenance of digit or letter strings as described. However, paradigms in which two tasks must be performed simultaneously (dual-task paradigms) also load on cognitive control resources, producing the same effects on distractor processing (Lavie et al. 2004; Boot, Brockmole & Simons, 2005).

Some contrary findings, in which working memory load had no effect on distractor processing, suggest that only salient distractors will capture attention even with high working memory load (Carmel, Fairnie & Lavie, 2012). A recent meta-analysis of 49 experiments from 26 studies (De Fockert, 2013) found that the effects of working memory load are predominantly in line with those shown in the studies by De Fockert et al. (2001) and Lavie et al. (2004). The contrasting effects of perceptual and cognitive load on distractor processing further reinforce the load theory hypothesis that exhaustion of a specific perceptual resource is a key factor in determining awareness. The independence of cognitive and perceptual load effects further indicates the role distinct underlying cognitive resources.

The respective roles of perceptual and cognitive control capacities were further investigated by Konstantinou et al. (Konstantinou & Lavie, 2013; Konstantinou, Bahrami, Rees & Lavie, 2012). Short-term memory maintenance of sensory information relies on the same sensory cortices that underlie perceptual processing (i.e. ‘sensory recruitment’; Postle, 2006). Based on this observation, the authors proposed that VSTM and perceptual load would draw on the same capacity and produce the same effects of exhausted capacity. In their investigations, they therefore manipulated VSTM load in addition to perceptual and cognitive control load. In these experiments, participants were presented with visual search tasks of either low or high perceptual load while also holding in memory some secondary information, similar to the paradigm used by Lavie et al. (2004). This time however, the memorized information could either take the form of a string of digits (cognitive control load) or else a set of coloured squares (VSTM load). As in the paradigm of Lavie et al. (2004), participants held this information in memory while performing a visual search task, then responded to a memory probe at the end of the trial (Figure 1.7). VSTM load significantly reduced detection sensitivity for peripheral targets during visual search. That is, holding visual displays in memory lead to similar effects to those of perceptual load, the opposite to those of cognitive control load.

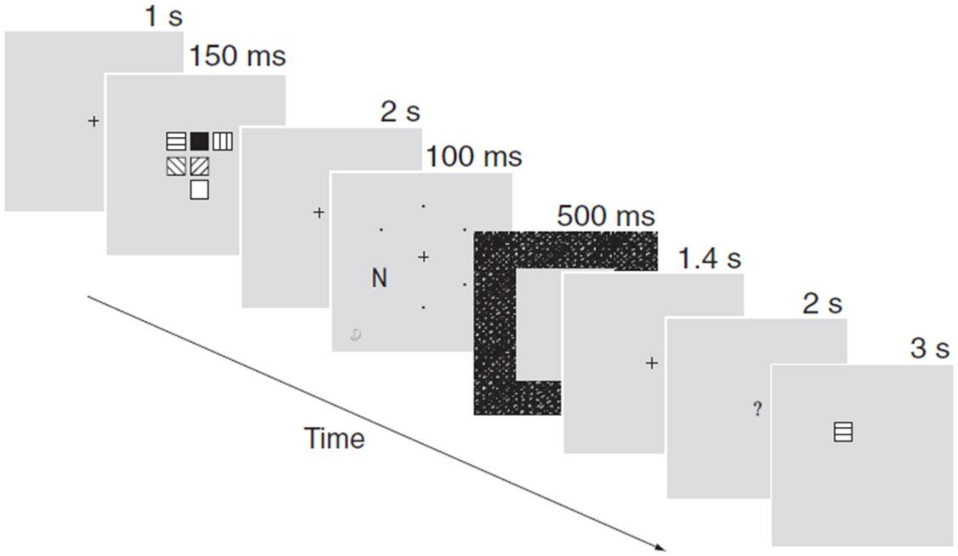

Figure 1.7 Example of the VSTM load paradigm employed by Konstantinou & Lavie (2013) in which participants memorize a set of coloured squares before performing a high or low load search in which they attempt to also detect a peripheral stimulus.

Perceptual capacity can therefore be loaded by processes which involve representation by sensory brain activity, be they online perception or maintenance of a perceptual representation which is no longer present. Cognitive control, on the other hand, is loaded by tasks requiring maintenance of abstract information or secondary task goals.

1.2.3 Defining the boundary between high and low perceptual load

Load effects are typically studied by comparing conditions of high versus low perceptual load. That is, conditions that exhaust the perceptual resources of all participants (or at least the vast majority) are compared to those that are clearly within capacity limits. However, in order to establish the nature of capacity limits, especially in the context of individual differences, it is necessary to use a more fine-grained approach. In the following subsection I will therefore describe some research into the specific point at which capacity is exhausted by different classes of stimuli and within certain participant populations.

Typically, studies seeking to establish more specific capacity limits have employed designs including conditions of ‘intermediate load’, in-between the standard high load and low load conditions. For example, Lavie and Cox (1997; Experiment 2) adapted the canonical letter search paradigm to include multiple set sizes, including conditions with zero, one, three or five non-targets in the search array. Their results showed that distractors caused significant interference in search performance for all set sizes below five. That is, distractor interference was essentially equivalent for set sizes up to around four and only for larger sets was this interference eliminated. A similar result was found by Lavie and Fox (2000) using a negative priming paradigm, showing that negative priming effects were only fully eliminated by relevant set sizes of more than four items.

In their investigation Lavie and Cox (1997) further found that the task conditions which eliminated distractor processing were the same as those which yielded inefficient visual search. In the visual search literature there is a well-established distinction between efficient and inefficient search (Wolfe, 2007; 2014; Treisman & Gelade, 1980). Efficient search occurs typically when the target stimulus can be identified on the basis of a single feature (e.g. colour or orientation) among homogeneous non-targets. These search conditions are considered ‘efficient’ as they yield very shallow or even flat response time slopes when plotted as a function of set size. That is, in a search which includes many non-targets the response time is no different from a search involving only a small number. Inefficient search on the other hand, occurs when search targets share features with non-targets and is characterized by a linear increase in response time corresponding to increases in set size. Efficient search is thought to represent a parallel processing of the search display, whereas inefficient search requires serial selection of each potential target (Treisman & Gelade, 1980). As discussed previously, in load theory, processing within perceptual capacity limits is thought to be parallel and automatic as in efficient search.

The findings of Lavie and Cox (1997) are supported by a recent investigation into the factors which determine distractor interference. Roper, Cosman and Vecera (2013) directly compared the search efficiency and the distractor interference effects yielded by a variety of different stimuli. Their stimuli were selected on the basis of similarity between the target and distractors as well as the homogeneity of the distractors themselves. Three stimulus types were therefore used (Figure 1.8): One in which a rotated ‘T’ shape was presented among ‘C’s (efficient search and low load), one in which the same target was presented among diagonally rotated ‘L’s (intermediate efficiency and load) and one in which the target (T) was presented among horizontally and vertically rotated ‘L’s (inefficient search and high load). In each condition the non-target stimuli were either presented in uniform orientation or in random orientation so that target/ distractor and distractor/ distractor similarity were manipulated independently. Their results showed that the same stimuli which yielded efficient search also yielded high levels of distractor interference. Specifically, similarity between the targets and the non-targets in the display was the key factor in determining both search efficiency and distractor processing. High levels of target/ distractor similarity lead to less efficient search and reduced distractor interference. The homogeneity of distractor stimuli on the other hand was only an important factor in determining search efficiency and distractor interference when target/ distractor similarity was high (i.e. in already intermediate or high load displays).

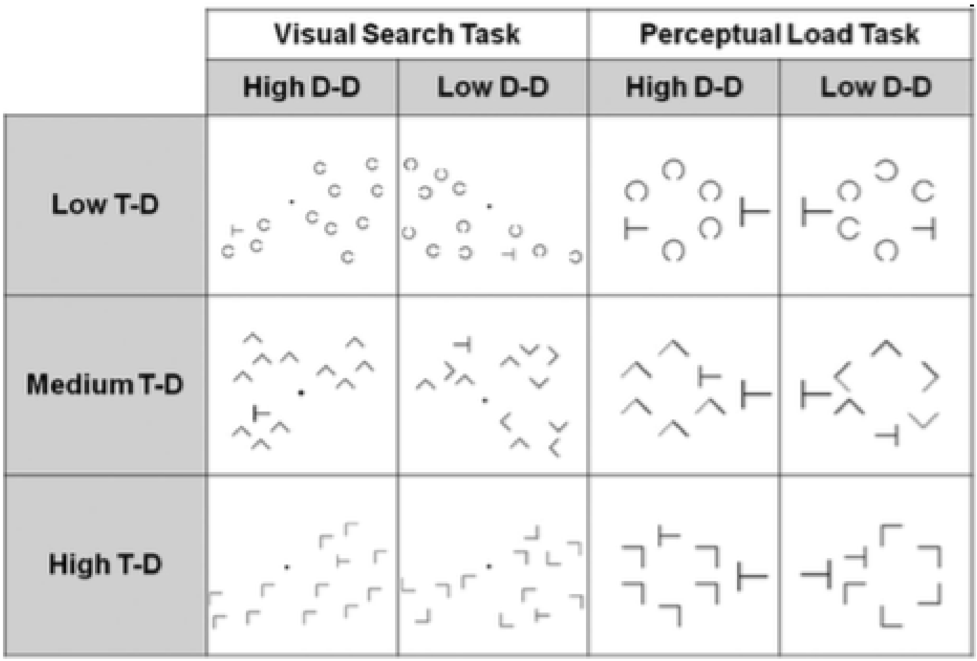

Figure 1.8 Example stimuli from the investigation by Roper et al. (2013) including visual search and perceptual load tasks with high and low distractor-distractor and target-distractor similarity

Thus, if a target can be selected on the basis of a single feature then it will facilitate parallel processing and will constitute low perceptual load. This explains why search among homogeneous non-targets (searching for an X among O's) constitutes low perceptual load, and is also supported by paradigms in which perceptual load is manipulated by means of the number of features which define a target (e.g. Schwartz et al. 2004; Carmel et al. 2011).

1.2.4 Variable capacity limits for specific stimuli and populations

The apparent perceptual capacity limit of approximately four items is in accordance with prior literature indicating similar capacity limits in attention demanding tasks (e.g. Yantis & Jones, 1991; Kahneman, Treisman & Gibbs, 1992; Pylyshyn, Burkell, Fisher & Sears, 1994). However, there is evidence that capacity for certain classes of stimuli may be less strictly limited. Although there has not been a great deal of research within the load theory literature into inter-individual variability in perceptual capacity and susceptibility to perceptual load, there is evidence that capacity is not necessarily fixed at four items for all people and all stimulus categories. Certain populations, discussed below, have apparently enhanced perceptual capacity either due to perceptual expertise or certain clinical conditions. For example Lavie, Ro and Russell (2003) found no effect of increased load on distraction from face stimuli during a name categorization task (similar to that used by De Fockert et al. 2001). In their investigation, relevant set sizes of up to eight names were not sufficient to eliminate distraction from face stimuli, whereas distraction from other images (e.g. musical instruments) was eliminated by sets over four as usual. This result could be interpreted as evidence that faces as a stimulus class are not subject to the same perceptual capacity limits as other stimuli. However, an alternative argument is that faces represent a stimulus class involving high levels of visual expertise (e.g. Bukach, Gaulthier & Tarr, 2006). A subsequent study (Ro, Friggel & Lavie, 2009) demonstrated that this explanation may apply to the results of Lavie et al. (2003). They used the same paradigm as the non-face distractor condition used by Lavie et al. (2003) but this time tested expert musicians. That is, participants with musical expertise performed a task in which they reported which type of musical instrument name was presented among irrelevant non-words while ignoring distractor images of musical instruments. The results replicated those of the face distractor condition in Lavie et al. (2003): Musical instrument images caused significant interference to task performance even under high perceptual load conditions. Thus the apparent increased perceptual capacity may be explained by stimulus specific visual expertise. At any rate these results demonstrate that perceptual load effects are subject to group differences between experts and non-expert observers as musicians were less susceptible than non-musicians to increased perceptual load.

There is evidence for similar apparent ‘enhancement’ of perceptual capacity among specific clinical populations, especially individuals diagnosed with Autism spectrum disorders. Some theories have suggested that an altered perceptual processing style may be a key factor underlying Autism: People with Autism appear to show a preference for perceptual details over holistic processing (Happe & Frith, 2006), and appear to be less subject to certain attentional capacity limits than the typical population (Mottron & Burack, 2001; Mottron, Dawson, Soulieres, Hubert & Burack, 2006). Accordingly, Remington, Swettenham, Campbell and Coleman (2009) found that participants with Autism were less susceptible to increased perceptual load than were typical participants. They presented both groups of participants with a letter search task with intermediate levels of load as used by Lavie and Fox (1997). That is, participant searched for a target letter (an ‘X’ or an ‘N’) among a variable number of non-target letters (zero, one, three or five) while ignoring flanking distractors. In their results, distractors caused significant search interference for all but the highest set size in participants with Autism; whereas distractor interference was eliminated with only three non-targets (i.e. a total search set size of 4 items) in the typical sample. People with Autism therefore appear have an enhanced perceptual capacity relative to the typical population.

In further investigations using similar paradigms, participants with Autism have been shown to experience reduced rates of inattentional blindness and load-induced blindness as compared to typical controls (Remington, Swettenham & Lavie, 2012; Swettenham et al. 2014). Participants with autism detected expected and unexpected peripheral stimuli with greater frequency and under higher load than their typical counterparts. These findings support the hypothesis that individuals with Autism have an enhanced perceptual capacity, rather than simply a reduced ability to suppress distractor processing.

A study by Baylis and Kritikos (2011) found equivalent results with a sample of participants who did not have Autism but scored highly on the ‘Autism Quotient’ questionnaire (AQ; Baron-Cohen, Wheelwright, Skinner, Martin & Clubley, 2001), which provides a scale of ‘Autistic traits’ in the typical population. As in the clinical population studied by Remington et al. (2009); participants with relatively more Autistic traits persisted in distractor processing at higher levels of perceptual load. Similarly, Rusconi and colleagues (Rusconi, McCrory & Viding, 2012; Rusconi, Ferri, Viding & Mitchener-Nissen, 2015) adapted questions from the AQ questionnaire for use as a screening tool for x-ray security personnel (the ‘XRIndex’). They found that a subset of questions selected from the AQ were predictive of performance in threat detection from x-ray images of vehicles and luggage. Autistic traits are therefore associated with both increased detection sensitivity for hard-to-identify stimuli as well as for distractors during search, two key indicators of high perceptual load. It is therefore possible that perceptual capacity may vary from person to person in much the same way that Autistic traits are thought to lie on a broad spectrum encapsulating the entire population (e.g. Baron-Cohen, 1995).

One study by Forster and Lavie (2007) found that individual differences in self-reported distractibility were significantly correlated with distractor interference under low load but not high load. That is, the cost associated with a response competing distractor versus a neutral distractor on low load trials was correlated with scores on the ‘Cognitive Failures Questionnaire’ (CFQ; Broadbent, Cooper, Fitzgerald & Parkes, 1982), which has been shown to measure a trait associated with various types of real world accidents such as car collisions (Larson & Merritt, 1991) and workplace accidents (Wallace & Vodanovich, 2003). This result was replicated in a more recent study by the same authors (Forster & Lavie, 2015), this time by measuring traits associated with attention deficit/ hyperactivity disorder (ADHD). The number of ADHD traits as measured using the childhood symptoms scale (Barkley &

Murphy, 1998) was significantly correlated with distractor processing in low load conditions, but not high load, as in the results of Forster and Lavie (2007).

The fact that higher daily life distractibility and ADHD traits were correlated only with distractor interference effects in low load conditions indicates that it is not perceptual capacity but rather the capacity for cognitive control which drives these relationships. In the low load condition, distractor processing proceeds automatically, and must therefore be suppressed by top-down executive control of attention. Thus, there is evidence for inter-individual variability in distractibility under low perceptual load, attributable to differences in cognitive control resources. There is also evidence for individual differences in perceptual capacity, associated with visual expertise and self-reported autistic traits. However, there is as yet little investigation into how these differences may relate to one another and to tasks beyond the standard load paradigms.

1.3 Capacity limits in other paradigms

Capacity limits of around three to four items have been reported in numerous paradigms beyond the load theory literature and various theories have proposed a common underlying capacity-limited resource. Given the hypothesis that a common resource underlies processing under perceptual demands generally this research is important to consider. In the following section I will therefore review some of the more prominent examples and describe theoretical frameworks for their shared capacity limits.

1.3.1 Visual short term memory capacity

One of the most prominent examples of capacity limits for visual processing is VSTM capacity. When participants are presented with a variable number of simple stimuli (e.g. coloured squares) and asked to hold them in memory for a brief period, their performance reaches a plateau at around three to four items. This capacity limit has been shown to apply to both very simple and relatively complex stimulus categories (e.g. Luck & Vogel, 1997; but see Bays, Catalano & Husain, 2009 for contrary evidence) and is reflected by equivalent plateaus in brain activity. For example, the amplitude of ‘contralateral delay activity’ (CDA; the electroencephalographic activity recorded over electrodes contralateral to the side on which stimuli were presented) is significantly increased during retention of larger set sizes in VSTM (Vogel & Machizawa, 2004). Furthermore, Vogel and Machizawa (2004) found that individual participant’s capacity limit in behavioural performance was significantly correlated with the point at which the amplitude of their CDA reached its plateau. A similar finding was reported by Todd, Fougnie and Marois (2005); using fMRI they found that VSTM load was associated with increased activity in the Temporo-Parietal Junction (TPJ) of the right hemisphere. This activity increased with increasing set size up to four items but not higher, mirroring the profile of the CDA. Todd et al. (2005) also found that rates of inattentional blindness were increased by VSTM load, providing further evidence that the underlying resource is necessary for online perception. As described previously, several studies have investigated the role of visual short-term memory within the load theory literature; demonstrating equivalent effects to those of perceptual load (Konstantinou et al. 2012; 2013; see section 1.3.2). These results, along with other research supporting the sensory recruitment hypothesis, indicate a shared resource underlying both VSTM and perceptual capacity.

Some recent findings suggest that cognitive control also plays a significant role in determining VSTM capacity limits. For example people with smaller VSTM capacity have been shown to involuntarily encode distractor stimuli which are ignored by those with greater capacity (Vogel, McCullough & Machizawa, 2005; Fukuda & Vogel, 2009). Capacity estimates increase with increasing set size up to around four items (Luck & Vogel, 1997), however, the plateau reached at around four items may not be entirely stable. Recent studies have shown that when people attempt to memorize larger set sizes their capacity can be reduced to below four items (Linke, Vincent-Grabovetsky, Mitchell & Cusack, 2011; Fukuda, Woodman & Vogel, 2015). Suggesting that VSTM capacity is at least in part limited by top-down cognitive control, which is necessary for effective selection of individual items in the memory set and avoiding ‘contamination’ from other items. In synthesis, the evidence appears to indicate that VSTM utilises perceptual resources (sensory recruitment) and that this utilisation is enacted by top-down cognitive control. In other words, although VSTM maintenance depends upon the same limited capacity resource as online perception (Konstantinou & Lavie, 2013), resulting in its four item limit; VSTM retention also involves further resources for top-down control of this capacity.

1.3.2 Multiple object tracking (MOT)

An equivalent limit is also apparent during covert tracking of moving objects in the MOT task (Pylyshyn & Storm, 1988). In this task, participants are presented with a set of homogeneous stimuli and instructed to track a subset of them as they move randomly around the screen, ignoring distractors. Performance generally indicates a capacity limit of between three and four items when tracking independent targets among matching distractors (Pylyshyn, 2001; Scholl, Pylyshyn & Feldman, 2001). The behavioural performance limit in MOT is associated with an equivalent plateau in contralateral delay activity (CDA) in the EEG as during VSTM maintenance: Drew and Vogel (2008) measured the EEG activity of participants while tracking different set sizes and found that, as with the VSTM task, CDA amplitude reached an asymptote when tracking load exceeded four items.

By combining MOT with the change blindness paradigm, Bahrami (2003) demonstrated that changes to tracking targets were more likely to be perceived than changes to non-targets, demonstrating that subjective awareness of changes and tracking capacity depend upon a common resource. The effects of tracking load on subjective awareness were further demonstrated by Tombu and Seiffert (2008), who found that increased difficulty in the MOT task lead to significantly reduced detection sensitivity for auditory tones, a demonstration similar to the ‘load-induced inattentional deafness’ reported by Raveh and Lavie (2015) and others. Further studies have demonstrated that probes (e.g. colour changes) are more likely to be detected if they occur on a target than on a non-target: For example, Shernstein, Agam and Sekuler (2011) recorded EEG activity associated with probes (white flashes) presented on targets and non-targets during tracking. They found that early ERP amplitude evoked by probes on non-targets was significantly lower than for probes on targets. Furthermore, the amplitude evoked by the probes was significantly reduced as a function of tracking set size such that responses to target and non-target probes were essentially equivalent when participants tracked four items. This result indicates that with increased tracking load the available perceptual resource was diminished, leading to reduced probe related activity. When capacity was exhausted by tracking four targets there was no remaining capacity available to process target probes preferentially and so the target/ distractor difference was eliminated.

Finally, MOT capacity is significantly correlated with visuospatial working memory capacity, even when controlling for contributions from executive control (Trick, Mutreja & Hunt, 2012). This suggests that a common resource other than cognitive control contributes to performance in the two tasks.

1.3.3 Visual enumeration and subitizing

When presented with a variable number of stimuli and instructed to report how many as quickly and accurately as possible, observers’ performance typically forms a characteristic ‘bilinear’ function (Figure 1.9). For small numbers, up to around four items, responses are typically very quick, accurate and unaffected by increases in set size – producing a flat response slope. Responses then become slower and less reliable with each additional item beyond sets of around four, forming a serial counting or estimation slope. This phenomenon has long been observed and the underlying process has been the subject of some considerable debate (Jevons, 1871; Kaufman, Lord, Reese & Volkmann 1949; Mandler & Shebo, 1982).

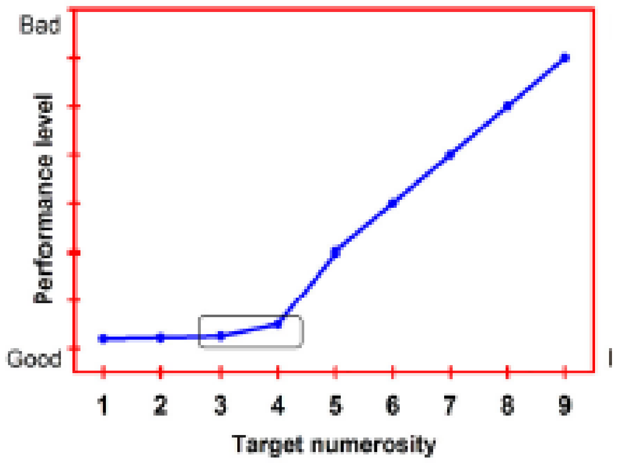

Figure 1.9 An example of the bilinear profile of subitizing and subsequent counting or estimation typically observed in visual enumeration tasks (from Mazza & Caramazza, 2015)

One explanation of the subitizing phenomenon describes a process specific to numerical estimation but common to all quantities, for which precision decreases with increasing set size in accordance with Weber's law (Dehaene & Changeux, 2007; Ross, 2003). This explanation has not been supported by more recent research however, which demonstrates independence of mechanisms for estimation of large and small set sizes and a lack of correlation between individual subitizing performance and that of higher number estimation (e.g. Revkin, Piazza, Izard, Cohen & Dehaene, 2008). Furthermore, the distinction between subitizing and other numerical processes is supported by neuroimaging evidence which indicates different patterns of activation associated with subitizing and counting or numerical estimation. For example posterior parietal activity was modulated by estimation of higher numerosities but not subitizing in an fMRI study by Piazza, Giacomini, Le Bihan and Dehaene (2003). Another study by Ansari, Lyons, Eimeren and Xu (2007) found that while the bilateral intra-parietal sulcus was associated with increased quantities in both symbolic and non-symbolic displays (i.e. Arabic numerals and randomly positioned dots respectively), activity in the right TPJ was specific to subitizing of non-symbolic displays (see also Cutini, Scatturin, Moro & Zorzi, 2014 for a similar result). Activation of the TPJ has also been shown to be specific to attentional effects within the subitizing range in subsequent research (Vetter, Butterworth & Bahrami, 2011).

A study by Demeyere, Rotshtein and Humphreys (2012) measured the subitizing capacity of brain lesion patients as well as typical controls in order to identify the structural correlates of subitizing and higher numerosity estimation. They found that a wide range of fronto-parietal locations were associated with deficits in enumeration performance generally, including parts of bilateral occipital and parietal cortices and right frontal cortex. Importantly, lesion damage to the left intraparietal sulcus (IPS) was selectively associated with impairments in non-subitizing performance (i.e. with larger numbers) whereas damage to earlier visual and right parietal areas (precuneus) was selectively associated with impaired subitizing.

These neuroimaging results support a distinction between subitizing and other forms of enumeration in terms of brain activity and structure. They also suggest a possible right parietal dominance in subitizing performance, which is in agreement with right hemisphere dominance in visual attention reported elsewhere (e.g. Heilman & Van Den Abel, 1980; Shulman et al. 2010). Thus, most recent evidence points toward a distinct, capacity-limited process underlying subitizing. Other evidence, discussed in the following subsection suggests that this capacity may be common generally to tasks involving perceptual load.

1.3.4 Theories of a common capacity for parallel object individuation

Pylyshyn and colleagues (Trick & Pylyshyn, 1993; 1994; Pylyshyn et al. 1994; Pylyshyn, 2001) proposed a mechanism for the parallel individuation of multiple distinct objects which underlies the capacity limits in subitizing, object tracking, visual search and VSTM. According to this theory a limited number of location indexes or ‘FINSTs’ (i.e. ‘fingers of instantiation’) are deployed at a preattentive stage to guide attention to a subset of task relevant stimuli. Indices are therefore not specific to numerical processing or any particular class of stimuli but shared by any task requiring simultaneous perception of multiple objects. Indices were thought to be preattentive due to the robustness of subitizing and MOT to the presence of distractors. As discussed, participants are able to effectively track targets in the MOT task even among large numbers of distractors as long as the number of targets does not exceed capacity. In visual enumeration tasks, people are able to subitize up to three or four prespecified items even if these targets are presented among non-target distractors, provided that distractors can easily be differentiated on the basis of some salient feature such as colour (Trick & Pylyshyn, 1993). In such situations, the same bilinear profile is observed implying parallel subitizing up to around three or four items. This is taken as evidence that attention was not necessary to differentiate targets from distractors.

There are clear parallels between the visual indices proposed by Pylyshyn and colleagues and perceptual capacity as described in load theory. Indices are thought to select a limited number of stimuli in parallel and to be deployed automatically to salient stimuli (Pylyshyn, 2001). Both perceptual capacity and visual indices are thought to depend on a distinct capacity which can be guided by top-down cognitive control (Lavie et al. 2004). However, the theories differ in their claims regarding the role of attention: indices are thought to be preattentive whereas perceptual capacity is thought to represent the capacity of selective attention itself. An alternative account of MOT described by Cavanagh and Alvarez (2005) suggests that capacity limits in tracking are the result of multifocal attention. They propose that attention can be split between up to four targets, or more precisely, two objects per hemisphere. The latter component of their theory was based on the observation that tracking is more effective when targets were distributed equally on both sides of the screen (Alvarez & Cavanagh, 2005). Recently, a growing body of research has undermined the idea of preattentive subitizing with evidence from a variety of experimental manipulations as I shall discuss in the following subsection.

1.3.4.1 Individuation requires attentional resources

Several recent investigations have demonstrated the requirement of attentional resources for subitizing by applying the ‘Attentional Blink’ paradigm. In this paradigm several stimuli are presented in rapid succession in one location on screen (a rapid serial visual presentation, or ‘RSVP’ paradigm). Stimuli presented within 700ms of a target in this stream often go unnoticed as attentional resources are still occupied by the target, resulting in a transient subjective blindness phenomenon (Raymond, Shapiro & Arnell, 1992).

This paradigm was applied to enumeration by numerous authors (Egeth, Leonard & Palomares, 2008; Olivers & Watson, 2008; Xu & Liu, 2008) in order to test the role of attention in subitizing. For example, Olivers and Watson (2008) presented a stream of letter stimuli at a rate of 133ms per letter. Participants were instructed to identify a target letter, which was presented in a unique colour, and then report the number of dots that was presented subsequently (e.g. Figure 1.10). Enumeration accuracy was significantly reduced when dots were presented during the blink period following a target compared to identical conditions with no target (and therefore no blink). A further experiment established that when letter targets and enumeration dots were presented in the opposite order, participants were able to subitize the dots, but this resulted in an attentional blink for the letter target. That is, subitizing the small number of dots consumed attentional resources, resulting in omission of the second target stimulus. Thus attentional resources are not only necessary for subitizing to occur they are also consumed by the process of subitizing.

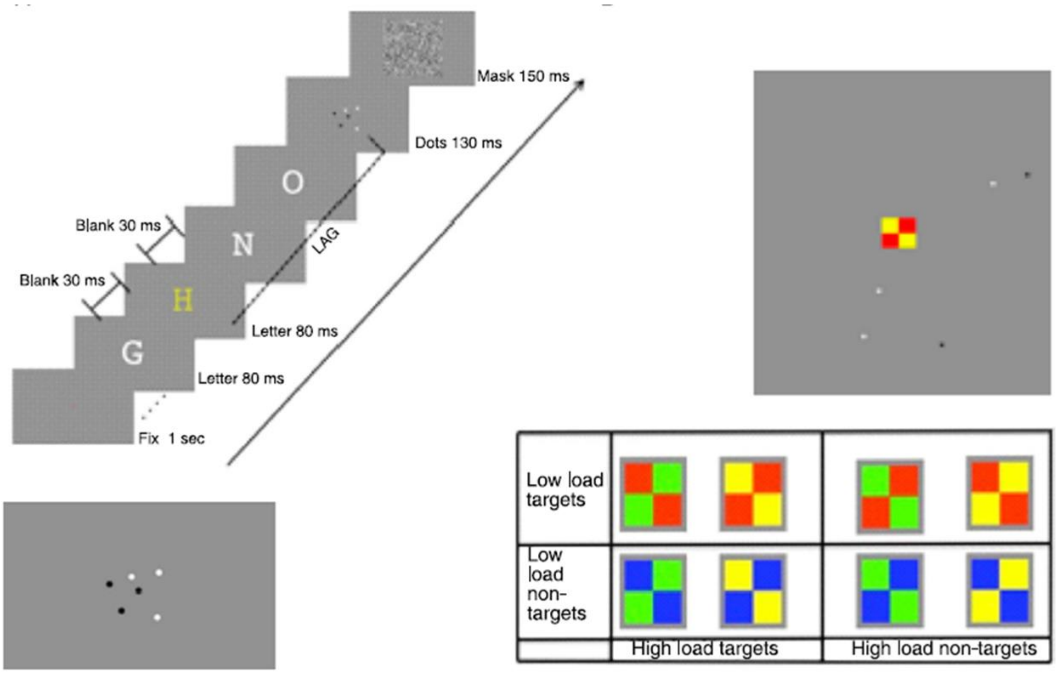

Figure 1.10 Tasks used (by Burr et al. 2010) to establish the necessity of attention for subitizing, including the attentional blink (left) and perceptual load (right) manipulations.

Burr, Turi and Anobile (2010) used a similar paradigm but included set sizes far beyond the subitizing range as well as smaller sets as used by Olivers and Watson (2008) and others. Due to the brief presentation times in the RSVP paradigm, participants were unable to serially count the dot stimuli one at a time and therefore had to rely on approximate estimation of these sets. Their results replicated those of previous researchers, finding that subitizing was negatively affected by the attentional blink. They also found that this effect was selective to subitizing: estimation performance of larger sets was unaffected by the attentional blink. This leads to the conclusion that while subitizing depends on attentional resources, coarser estimation of larger quantities may not.

In a second experiment Burr et al. (2010; see also Vetter, Butterworth & Bahrami, 2008) manipulated the availability of spatial attention (as opposed to temporal attention as in the RSVP paradigm). In this experiment participants were required to identify targets on the basis of either a single feature (colour) or a conjunction of features (colour and orientation) in a manipulation very similar to those used in load theory literature (e.g. Schwartz et al. 2004; Carmel et al. 2011, See section 1.2). While performing this target identification task, participants also attempted to enumerate the number of dots presented in a ‘cloud’ surrounding the target (Figure 1.10). Once again, when attentional resources were consumed by the central task, subitizing could not occur but estimation of larger sets was unaffected.

Another study used the inattentional blindness paradigm to demonstrate the necessity of attentional resources for subitizing: Railo, Koivisto, Revonsuo and Hannula (2008) used the line-length judgement task described earlier (Mack & Rock, 1998; section 1.2.1) but instead of presenting a single critical stimulus they instead presented a variable number of dots and asked participants how many had been present. On the critical trial, when participants did not direct attention to the dots (as they were not expecting to see them) they were significantly less accurate in their numerical report than in a full attention condition. This was true for set sizes as low as two, even though participants noticed that at least one critical stimulus had been present (i.e. they were not entirely ‘blind’ to the stimuli). Thus providing further evidence that subitizing cannot occur without attention and suggesting that the perceptual capacity underlying subitizing is common to subjective blindness phenomena as well as perceptual load manipulations.

Burr and colleagues (Burr & Ross, 2008; Ross & Burr, 2010; Burr et al. 2010) proposed that numerosity represents a basic visual feature, similar to colour or orientation. They suggest that while subitizing represents a limited capacity for individuation of stimuli, estimation of numerosity can still be performed in the absence of attention in much the same way as has been suggested for ‘summary statistics’ of basic visual features (e.g. Ward, Bear & Scholl, 2016). This hypothesis was formulated based on evidence that numerosity judgements are subject to adaptation in the same way as, and independently of, other basic visual features. For example, participants who are perceptually adapted to larger numbers report smaller average numerosity than those adapted to smaller numbers (Burr & Ross, 2008).

Current theories are therefore largely in agreement that subitizing represents a distinct process to counting or estimation, one which requires attention. This resource can be exhausted by manipulations of perceptual load and subjective blindness phenomena (inattentional blindness and the attentional blink). Thus, subitizing does not depend upon preattentive indexing as described by Pylyshyn and colleagues. However, the concept of a limited capacity for parallel object individuation (which requires attention) remains a popular interpretation (Ester et al. 2012; Piazza, Fumarola, Chinello & Melcher, 2011; Mazza & Caramazza, 2015).

Recent evidence for this hypothesis has come from EEG research, which has shown that subitizing a larger number of stimuli is associated with increased amplitude in ERP components associated with attentive selection. Specifically the CDA component observed in both the VSTM and MOT tasks has a similar profile in subitizing tasks – increasing in amplitude for each additional target item up to a plateau around four items (Ester et al. 2012; Pagano & Mazza, 2012). Furthermore, subitizing is also associated with a similar set-size dependent increase in the amplitude of the N2pc component, a negative deflection of the EEG around 200ms following stimulus onset. The N2pc is well established to be involved in attentional orienting and selection (e.g. Eimer, 1996; Luck, 2005). Ester et al. (2012) presented lateralized enumeration displays while recording participant's EEG activity and found that the amplitude of the N2pc increased with increasing set size, reaching a plateau at the behaviourally measured capacity limit. This provides evidence that subitizing represents the maximal capacity for selection of independent stimuli in parallel.

This hypothesis is also supported by findings showing that the capacity for subitizing can be loaded by tasks which require individuation of objects other than the subitizing targets. For example, Piazza et al. (2011) found that increased VSTM load lead to reductions in subitizing range. When participants maintained sets of coloured squares in VSTM and enumerated stimuli during the retention interval, their subitizing range was negatively impacted by VSTM load at a rate of approximately one to one. That is, for each additional item in memory, subitizing capacity was reduced by approximately one item, lending support to the hypothesis that both processes depend upon a shared capacity (Cutini & Bonato, 2012). In their results Piazza et al. (2011) also demonstrated that VSTM capacity was significantly correlated with individual subitizing capacity, but not with estimation of larger sets, supporting the distinction between the capacity for individuation and general number sense.

In a similar study, Chesney and Haladjian (2011) combined enumeration with an object tracking task (Figure 1.11). They presented participants with a standard MOT task but during the tracking interval an additional set of squares were presented amongst the moving dots, which participants were instructed to enumerate. Increased tracking load in the MOT task was associated with decreased capacity for subitizing and the detriment to subitizing capacity by tracking load was approximately one to one, as in the results reported by Piazza et al (2011).

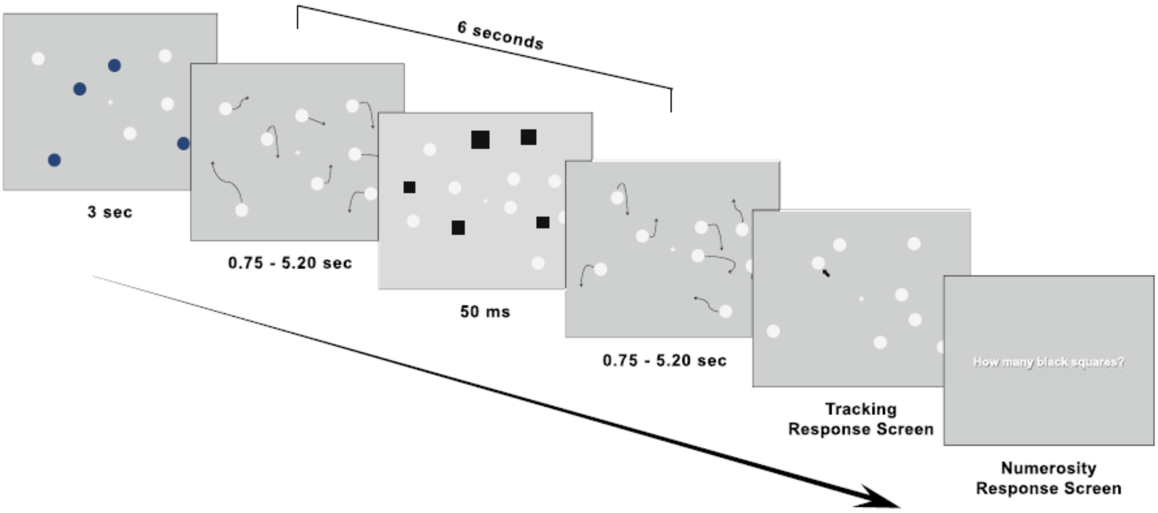

Figure 1.11 A schematic of the combined MOT and enumeration paradigm employed by Chesney and Haladjian (2011).

Parallel individuation has therefore been shown to be sensitive to the two primary manipulations of perceptual load: task-relevant set size (Chesney & Haladjian, 2012; Piazza et al. 2011) and target discrimination complexity (Vetter et al. 2008; Burr et al. 2010). This provides some support for the hypothesis that subitizing, MOT, VSTM and perceptual capacity reflect the same underlying resource. However, the studies described above used dual-task paradigms in which participants were required to actively attend to two ongoing task demands. Dual task demands involve cognitive load, placing more demands on the ability to maintain task priorities (discussed above, see section 1.2.2; Boot et al. 2005; De Fockert, 2013; Lavie et al. 2004), and so it is possible that the effects of these studies may be in some way attributable to the capacity of working memory and cognitive control resources. This is unlikely, given evidence from a study by Tuholski, Engle and Bayliss (2001), who found that working memory capacity was not associated with any differences in subitizing capacity but did involve better performance with larger number estimation. That is, they identified participants with high and low working memory capacity using the OSPAN ('Operation Span') test, which involves memory maintenance as well as task-switching. Individuals with greater working memory span performed no better than those with smaller capacity when enumerating small numbers. However, the high capacity participants did perform better in estimation of larger set sizes, indicating that although cognitive control has a role in enumeration performance subitizing depends upon an independent, perceptual, resource.

1.4 Individual differences and brain structure

As discussed in detail throughout section 1.2.2, load theory provides considerable evidence for a distinction between perceptual and cognitive load and for distinct, limited-capacity resources underlying perceptual and executive processing. The hypothesis that a common capacity underlies perceptual processing in general leads to the prediction that common effects of different sources of load should be observed in the brain. Furthermore, if inter-individual variability in capacity represents a stable trait then this variability should be manifested in the brain. In the following section I will therefore outline neuroimaging evidence for distinct correlates of perceptual capacity and describe methods for identifying neural sources of individual performance differences.

The implications of load theory to brain activity are straightforward: Activity related to task irrelevant distractor stimuli or secondary targets should be reduced or eliminated by increased perceptual load. The first study to test this hypothesis was described by Rees, Frith and Lavie (1997), who presented irrelevant moving stimuli surrounding a central task of either low or high load. Their results demonstrated that increased load in the central task lead to significant reductions in motion-related sensory brain activity. Various other studies have since shown load-dependent effects of distractor stimuli in category specific brain areas (e.g. De Fockert et al. 2001). Further studies show that perceptual load leads to decreased activity in early visual cortex (Schwartz et al. 2004), even in response to stimuli that do not reach conscious awareness (Bahrami, Lavie & Rees, 2007). In addition to MRI measures, electrophysiological evidence shows that temporally early brain responses associated with task-irrelevant stimuli are significantly reduced by increased perceptual task load (e.g. Handy et al. 2001; Parks, Beck & Kramer, 2013).

Perceptual load therefore affects brain activity at very early processing stages, however, load effects are also observed in higher cortical regions, including parietal and frontal cortex (Schwartz et al. 2004; Beck et al. 2001). The right parietal cortex in particular was found to play a causal role in determining change blindness under load (Beck et al. 2005), mirroring the role of right parietal regions in subitizing and other paradigms described above. However, simply observing that a region is activated during a task does not necessarily indicate that processing in said region is the source of individual performance differences. In order to identify the locus of perceptual and executive capacities in the brain it is necessary to take an individual differences approach. One way to achieve this is through structural brain imaging and analysis using techniques such as Voxel-Based Morphometry (VBM; Ashburner & Friston 2000; 2001).

The gross morphological structures of individual brains differ significantly in terms of their overall and relative size, shape and the positions of brain regions. VBM focuses on differences in the volume of different tissue types throughout the brain; raw images are segmented into specific tissue classes representing grey and white matter (along with others such as bone and cerebrospinal fluid). These segmented images are then spatially normalized such that the gross differences in position and size of brain structures are removed. By analysing the intensity of the resulting images it is therefore possible to obtain a measure of grey (or white) matter volume for a given brain location across a sample of individuals. This measure of tissue volume provides an analogue of cell density in each voxel and can then be correlated with other (behavioural) measures of cognitive constructs (Kanai & Rees, 2011; Collins et al. 2010; Ashburner & Friston, 2000; 2001).

VBM has often been used to compare brains of experts and non-experts in a given task or stimulus; large differences have been identified in association with musical expertise (Gaser & Schalug, 2003) as well as language expertise in bilinguals (Mechelli et al. 2004) and navigational expertise in taxi drivers (Maguire et al. 2000). More relevant to the current thesis, a study by Tanaka et al. (2013) found that expert action video-game players (i.e. competitors in a professional tournament) had significantly increased VSTM capacities as well as significantly greater right parietal grey matter volume. This fits well with previous functional imaging evidence that VSTM load is associated with parietal (TPJ) activity (Todd et al. 2005). This also provides some initial evidence that individual differences in perceptual capacity can manifest in brain structure. As discussed above, a VBM study by Demeyere et al. (2012) established structure of the right and left parietal cortices as being selectively predictive of subitizing and estimation performance among neuropsychological patients.

VBM is not only used to compare expert and clinical populations however. Further research has established grey matter differences within the general population associated with a range of behavioural measures. For example, the perceptual strength of various visual illusions has been associated with early visual cortical structure (e.g. Schwarzkopf, Song & Rees, 2011; de Haas, Kanai, Jalkanen & Rees, 2012). One study by Kanai, Dong, Bahrami and Rees (2011) identified brain structures associated with attentional capture in daily life as measured by the cognitive failures questionnaire. They found that grey matter density in the left superior parietal lobule (SPL) was significantly correlated with CFQ scores, suggesting that this structure is involved in either stimulus driven perceptual processing or the exercise of top-down control on distractor processing. A follow-up study using magnetic stimulation to impair activity in this area confirmed that left SPL stimulation lead to increased distraction in a lab-based visual search task. The combined structural and stimulation data therefore provided robust evidence for the role of the left SPL in individual differences in top-down control of distractor processing.

Research has selectively associated attentional capacities for alerting and executive control (based on the Attention Network Test – 'ANT'; Fan et al. 2005) with distinct neuroanatomical correlates. Specifically, executive control was positively correlated with right inferior and left medial frontal cortex as well as the anterior cingulate whereas alerting was negatively correlated with left parietal grey matter (Westlye, Grydeland, Walhovd & Fjell, 2011; Hao et al. 2015). These structural correlates reflect similar brain regions to those identified with functional imaging studies of ANT measures (e.g. Fan, McCandliss, Fossella, Flombaum & Posner, 2005), and support the conclusion that the underlying capacities are associated with distinct brain structures.

There is thus considerable evidence for structural correlates of individual differences in top-down control of attention as well as other cognitive constructs from the VBM literature. There is considerably less evidence regarding measures of perceptual capacity, which according to the hypotheses outlined throughout this thesis should be associated with common brain structures, distinct from those associated with cognitive control. Individual differences in behavioural measures of capacity such as MOT, Subitizing and VSTM have frequently been linked to differences in brain activity, such as ERP amplitude over posterior (occipital and parietal) cortex and fMRI measured activity in parietal cortex (Vogel et al. 2005, Todd et al. 2005). There is good reason therefore to predict individual differences in the brain associated with behavioural capacity limits.

1.5 General methodology

In this thesis I used an individual differences approach to investigate perceptual capacity as a construct common to various diverse paradigms. In Chapter 2 I applied the load-contingent distractor interference paradigm to an enumeration task; participants performed an enumeration task while ignoring distractors. However, load on perceptual capacity was varied by the set size of the enumeration task (which included one to nine targets to enumerate).

Experiments in all of the following chapters subsequently utilized a visual enumeration paradigm in conjunction with various other tasks to establish common variance in behavioural performance and, in Chapter 5, brain structure. As discussed earlier, subitizing is typically measured by identifying the point at which performance becomes negatively affected by increasing set size. This can be measured by means of response accuracy or response times; in all but one experiment (Experiment 3) I used response accuracy as the measure of interest. Thus, the subitizing capacity of any one participant was defined as the point at which their accuracy transitioned from a flat to a negative slope with increasing set size.

In Chapter 3 I used a standard visual enumeration task with no distractor stimuli, in addition to this task, participants also completed a load-induced blindness task (Experiment 3) and a change blindness task (Experiment 4). I investigated common variance between performance measures on these tasks with multiple regression, using both subitizing and non-subitizing performance as predictors of awareness. In Chapter 4 I used a similar approach but administered a broader range of tasks to participants. Here, in addition to the enumeration and change blindness tasks, I also administered a series of working memory span tasks as well as an object tracking task.

In Chapter 5 I present data from a structural imaging experiment. Participants in this experiment completed the same tasks as those used in Chapter 4 but also provided structural MRI brain scans. Behavioural performance measures were then used as predictors of regional grey matter density using VBM analyses.

Chapter 2

Distractor processing during visual enumeration

2.1 Chapter Introduction

As discussed in the General Introduction (Section 1.2), the effects of perceptual load have been most extensively studied using paradigms in which load is manipulated and distractor interference effects are measured. The results of studies using this response competition paradigm typically show that peripheral distractor stimuli cause significant interference to performance of a central task, but only in conditions of low perceptual load. Originally, distractors shared the identity of task-relevant target letters (e.g. Lavie, 1995) but more recent demonstrations have further established this effect when distractor stimuli are ‘entirely irrelevant’ to the task (i.e. images of cartoon characters in a letter search task; Forster & Lavie, 2008).

If as argued in the General Introduction, perceptual capacity underlies subitizing, then this leads to the prediction that load effects should be replicated in an enumeration task. That is, distractors should cause significant interference within the subitizing range but this interference should be eliminated when subitizing capacity is exhausted. There is limited previous research regarding distractor processing and enumeration. Trick and Pylyshyn (1993) demonstrated that subitizing still occurs when an enumeration task includes non-target stimuli, as long as they differ from the target stimuli in some key feature dimension. If targets do not ‘pop-out’ from among non-targets then subitizing does not occur. That is, provided the targets can be selected efficiently subitizing can still occur, mirroring the distinction between efficient and inefficient visual search (Treisman & Gelade, 1980).

Vetter et al (2008) and Burr et al. (2011), applied load to visual enumeration using a dual task paradigm which involved detection of targets which were defined by either a single feature (colour – low load) or a conjunction of features (colour and orientation - high load). They found that increased load on the secondary task significantly affected performance within the subitizing range. However, dual-task paradigms increase demands on central cognitive resources (Boot et al. 2005; Fougnie & Marois, 2006) and do not provide insight into the nature of automatic distractor processing predicted by load theory. Load theory predicts that stimuli will unavoidably be selected provided there is available perceptual capacity and will fail to attract attention if capacity is exhausted. To truly establish this it is necessary to use distractor paradigms in which participants do not intentionally direct attention to anything other than the target stimuli (enumeration targets in this case). Furthermore, these studies did not investigate the role of individual differences in subitizing capacity.

In this chapter, I used a visual enumeration task which included the occasional (one third of trials) presentation of an irrelevant distractor image, which participants were instructed to ignore entirely. Furthermore, I assessed the contribution of individual differences to these results by estimating individual subitizing capacity limits and comparing ‘high capacity’ versus ‘low capacity’ quartiles in terms of their level of distraction. Somewhat counter-intuitively, higher capacity individuals are predicted to persist in distractor processing at higher set sizes compared to low capacity individuals, as their capacity for encoding stimuli is not yet exhausted.

2.2 Experiment 1

Participants in Experiment 1 were presented with a visual enumeration task which included occasional distractor stimuli. A set of black and white striped patches were presented, a variable number of which were brighter and horizontally oriented while others were dim and vertically oriented. Participants were asked to report the number of bright, horizontal patches and ignore dim vertical patches. On one third of trials a cartoon image similar to those used by Forster and Lavie (2008) was presented at fixation, participants were instructed to ignore these images.

Based on prior load theory literature, I predicted that distractors would cause significant interference in enumeration performance, but this effect would be limited to the subitizing range of around four items. Furthermore, I predicted that the influence of distractors would be dependent upon individual differences in subitizing capacity.

2.2.1 Method

Participants

Participants were first year undergraduate psychology students at UCL who took part in exchange for credit in a practical lab demonstration. A total of n = 84 students participated, 69 were female, aged 18-23 (*M* = 19.13, SD = 1.07). All participants reported normal or corrected to normal vision.

Stimuli and procedure

The experimental task was prepared and presented in Matlab (Mathworks, Inc., Natick, MA) using the Cogent toolbox (www.vislab.ucl.ac.uk/cogent.php) on one of 29 identical PC's with 15-inch flat screen monitors. Participants were seated in small testing cubicles approximately 60cm distance from the computer screen.

On each trial, a central fixation cross appeared for 1,000ms followed by a stimulus display for 200ms, this was then followed immediately by a response screen with a visual mask for a further 5,000ms or until the participant made a response. On one third of trials an image of a cartoon character appeared in the centre of the stimulus display, at the same time and for the same duration as the enumeration stimuli.

Participants responded by pressing a button from 1-9 on the keyboard number pad to indicate how many targets had been presented; responses could be made at any time following the initial presentation of the stimuli. Participants were instructed to ignore the distractor images entirely.

The stimulus display consisted of 11, 12 or 13 striped black and white circular patches, subtending 2.4 degrees of visual angle, arranged in a ring 9 degrees in diameter around the centre of the screen. On each trial a variable number of ‘target’ patches were presented which had horizontal stripes and a 50% brighter contrast than non-targets (which were vertically striped with a contrast of 50%). The distractor image was one of six cartoon characters (Mickey Mouse, Daffy Duck, Spongebob Squarepants, Pikachu, Spiderman and Superman) in a black square, the square subtended 4.8 degrees; the cartoon character was approximately 2.2 by 2.5 degrees. The visual mask which followed the stimulus display was made up of 24 black and 24 white overlapping circles arranged in random order in a ring covering the same area as the enumeration stimuli.

The number of target stimuli (1-9), the total number of stimuli (11-13) and the presence (or absence) of a distractor were counterbalanced such that there was an equal number of trials with any combination of these factors in each block. Trials were presented in random order throughout each block. The variable number of total stimuli served to ensure that the number of non-targets cannot be used to determine the number of targets in higher set sizes (i.e. by enumerating the smaller number of non-targets and subtracting this from the known total).

After one practice block of 10 trials, participants completed four experimental blocks of 81 trials, taking a self-paced break in-between blocks.

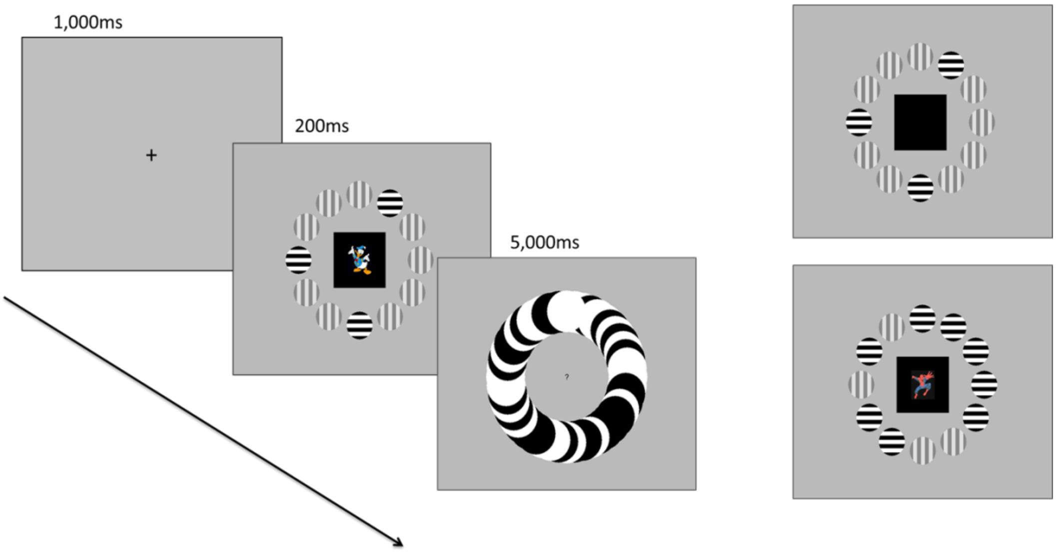

Figure 2.1 Left: A typical trial in the enumeration task of Experiment 1. Participants attempt to report the number of bright, horizontally oriented circles while ignoring the cartoon image, which is present on one third of trials. Right: An example of a trial in which no distractor is present (top) and an example of a trial with a larger set size (bottom).

2.2.3 Results

Task performance

The enumeration task in Experiment 1 included a visual mask to inhibit serial counting of stimuli from a visual afterimage. In this variety of enumeration task, accuracy at each set size is typically the variable analysed. Participants were excluded from analysis if their response accuracy was below 60% correct on the lowest set size of the enumeration task on trials where no distractor was present. This resulted in the exclusion of 6 participants, the final sample analysed was therefore n = 78 participants, 63 of whom were female, aged 18-23 (M = 19.14, SD = 1.26).

Table 2.1 contains the average enumeration task accuracy as a function of set size and distractor condition for set sizes one to eight (set size nine is excluded to avoid ‘end effects’ caused by participants guessing the maximum set size on supra-capacity trials).

	Distractor absent		**Distractor present**	
Set size	**Average accuracy (% correct)**	**SD**	**Average accuracy (% correct**	**SD**
1	97.09	4.19	88.44	11.75
2	96.85	4.30	88.41	16.31
3	92.33	7.28	84.15	13.51
4	77.81	15.63	68.82	19.98
5	58.37	17.86	57.88	25.11
6	44.67	14.99	42.12	23.52
7	27.78	13.30	31.29	23.84
8	25.35	15.17	23.99	22.97

Table 2.1 Average accuracy for each set size in the enumeration task of Experiment 1 for trials with and without distractor stimuli

Accuracy at each set size was entered into a 2x8 repeated measures ANOVA with within-subjects factors of distractor (present or absent) and set size (1-8). There was a significant main effect of set size (F(7,71)= 211.57, p < .001, η_p^2 = .95), indicating that accuracy was lower when enumerating larger sets. There was a significant main effect of distractor condition (F(1,77) = 23.23, p < .001, η_p^2 = .23), indicating that accuracy was lower when a distractor stimulus was present. Crucially, there was a significant interaction between distractor presence and set size (F(7,71) = 5.33, p < .001, η_p^2 = .34). As can be seen in Figure 2.2, responses were less accurate in the presence of a distractor but only at lower set sizes.

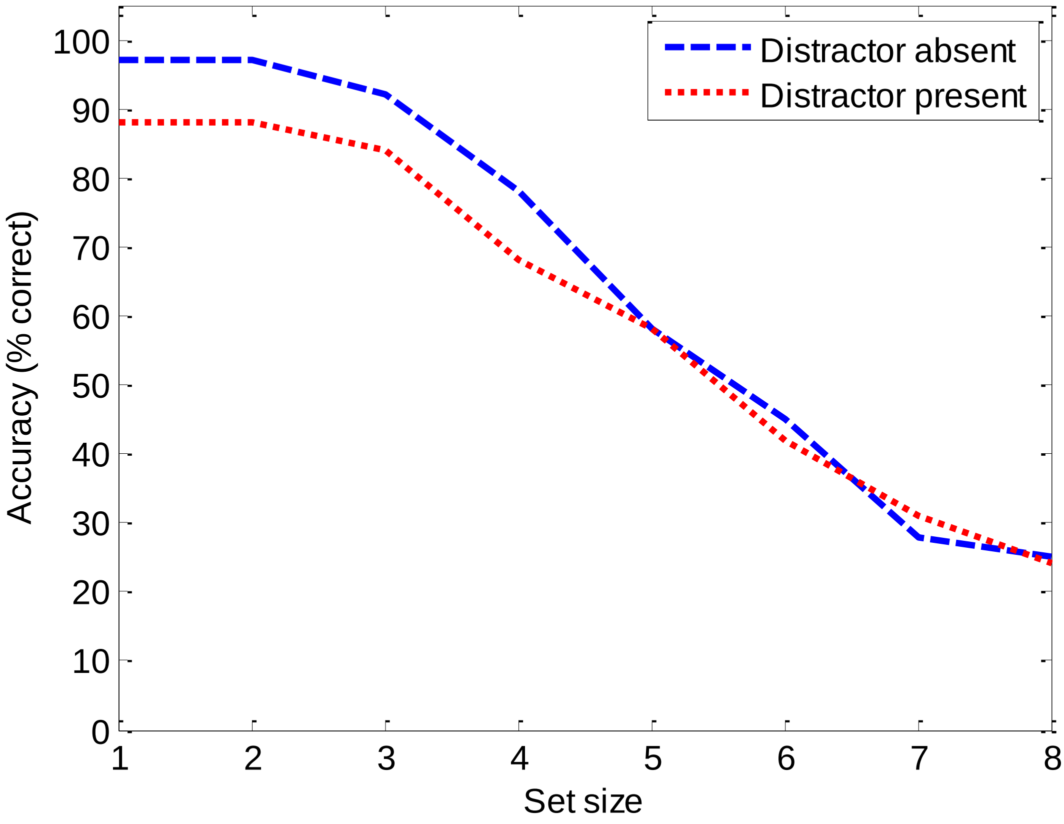

Figure 2.2 Enumeration accuracy plotted as a function of set size for trials without distractors (blue dashed line) and trials with distractors (red dotted line).

The effect of distractor condition was significant at set sizes 1-4 (Set size 1: t(77) = -6.81, p < .001; Set size 2: t(77) = -4.70, p < .001; Set size 3: t(77) = -5.37, p < .001; Set size 4: t(77) = -5.13, p < .001) but not any higher set size (all p's > .1), the significant effects withstood Bonferroni correction for multiple (8) comparisons.

Individual differences

According to load theory, distractors should only be processed within perceptual capacity limits. If subitizing represents perceptual capacity then distractors should only interfere with task performance within capacity limits for any given individual. This is supported by the experimental findings presented above, however, there is evidence that subitizing range (and perceptual capacity) varies from person to person (see General Introduction, section 1.3.4). Thus, individuals with higher subitizing capacity should remain prone to distraction at higher set sizes than low capacity individuals.

In order to identify the subitizing capacity for each participant, a bilinear function was fit to their accuracy at each set size for trials with no distractor stimulus. The function consisted of two linear components, the first with a flat slope and the second with a negative slope. The function used starting values of 90% intercept and 0% slope for the first line and -15% for the slope of the second line. Each integer set size value was tested as a candidate breakpoint for the function using these starting values. The value which fit with the least error was then taken as a starting point and parameters were varied from -1 to +1 of that value using Matlab's fminsearch function to find the best-fitting slope and intercepts (see Green & Bavelier, 2006 and Howe, 2017 for similar procedures). The average RMSE of the function fit to the data was 7.78 (SD = 4.04), average adjusted R^2 was .79 (SD = .20). Thus the function appeared to fit the data well, predicting observed scores with very little error. The point at which the two linear components of the function intersected was taken as the number of items that could be subitized by that participant. The average subitizing capacity across the sample was 3.20 (SD = 0.85, Range: 1.6 – 5.3), in line with capacity estimates of 3-4 items established in previous research. The sample was split into upper and lower capacity quartiles based on estimated subitizing range. The low capacity quartile had an average subitizing range of 2.29 (SD = .27, Range: 1.6 – 2.6), the high capacity quartile had an average capacity of 4.30 (SD = .48, Range: 3.7 – 5.3).

According to load theory, for low capacity individuals the effect of distractors should be eliminated by smaller set sizes than average as their capacity would already be exhausted. Those with higher than average capacity should still have spare perceptual resources available to process distractors at set sizes 3 or even 4.Thus there should be a significant decrease in distractor interference from sets 1-2 to sets 3-4 for the low capacity quartile but not for the high capacity quartile.

Distractor cost scores (accuracy when distractors were present subtracted from accuracy without distractors) for the low and high capacity quartiles were entered into a 2x2 ANOVA with set size (low: 1-2 items; high: 3-4 items) as a within subjects factor and quartile group (high vs. low) as a between subjects factor. The main effect of set size was significant (F(1,43) = 5.23, p < .05) and there was a significant interaction between set size and quartile group (F(1,43) = 9.99, p < .01, η_p^2 = .19).

There was a significant change in distractor cost from low set sizes (1-2) to higher set sizes (3-4) for the low capacity quartile (t(22) = 3.24, p<.01), indicating that capacity was exhausted beyond 2 items for these participants. There was no significant change in distractor cost for the high capacity participants (p>.05), indicating that distractors were still selected at the set sizes bordering average capacity limit.

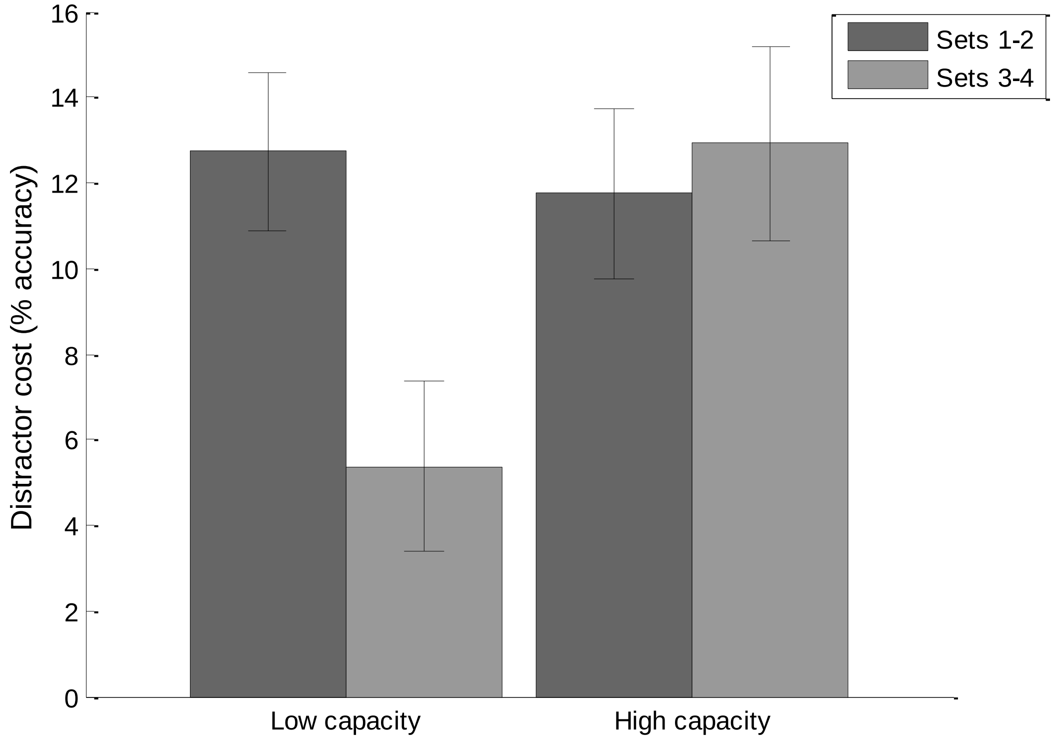

Figure 2.3 A bar graph for the comparison of high- and low-capacity quartiles in terms of distractor cost averaged over sets one-two and sets three-four in Experiment 1.

2.2.4 Conclusions

The results of Experiment 1 are compatible with the load theory prediction that distractors will be automatically processed within capacity limits (subitizing) but not when capacity is exhausted (higher set sizes). Furthermore, the finding that higher capacity individuals persisted in distractor processing at higher set sizes than those with lower capacity supports the hypothesis that perceptual capacity is subject to inter-individual variability within a typically developed student sample and that the subitizing range can be used as a measure of capacity.

2.3 Experiment 2

The design of Experiment 1 did not allow for measurement of response times as the brief display and subsequent mask resulted in increasingly low accuracy at higher set sizes. It is possible that participants may continue to process distractors even beyond the subitizing range if they had been capable of maintaining accurate performance. Thus, in Experiment 2 I used a similar paradigm with a longer response period and increased opportunity for participants to process stimuli at higher set sizes. This time, enumeration stimuli were white squares which contrasted strongly with their (black) background and no visual mask was used. Participants were encouraged to respond as quickly as they could to encourage subitizing when possible. According to load theory, distractor processing should be eliminated by exhausting capacity regardless of these changes and so the results of Experiment 1 should be replicated in Experiment 2, but with the distractor effect evident in response time rather than response accuracy.

2.3.1 Method

Participants

Once again participants were first year undergraduate psychology students at UCL, they took part for course credit in a ‘lab class’ demonstration (Note: this was a separate academic year and none of the same students participated in both experiments). The total sample was n = 88, aged 18-21 the average age was *M* = 18.88 (SD = 0.86), 71 participants were female.

Stimuli and procedure

Once again, the task was prepared and presented in Matlab (Mathworks, Inc., Natick, MA) using the Cogent toolbox (www.vislab.ucl.ac.uk/cogent.php). The testing procedure was the same as in Experiment 1.

The enumeration task used in Experiment 2 was similar to that used in Experiment 1 but used different enumeration stimuli and did not include a visual mask. On each trial, a fixation cross was presented for 1,000ms which was followed by a stimulus display which remained on-screen for 200ms. A blank screen followed immediately after the stimulus display and persisted for up to 7,000ms until a response was made, there was no visual mask and participants were encouraged to respond as quickly as possible after seeing the stimulus. On one third of trials a cartoon distractor image was presented in the centre of the screen at the same time and for the same duration as the enumeration stimuli.

Participants were instructed to respond by pressing a key on the number pad of the keyboard as in Experiment 1, the top row (‘Num Lock’, ‘/’ and ‘*’) keys were repurposed for numbers 10-12 with numbered stickers on the keys.

The stimuli to be enumerated in this task were 1-12 white squares arranged in random positions of an invisible ring (with a diameter of 10.9 degrees) around the centre of the screen. In one condition the squares were all of uniform size on a given trial but constrained such that the overall area of the squares was 1.46, 1.94 or 2.5 degrees on any given trial. In another condition the squares were of variable size on each trial and the total area of the squares was not controlled. The two conditions ensured that for half of the participants the total amount of screen saturation was not a clue to the number of squares present and for half the participants the size of any individual square was not a clue to the total number. The distractor image subtended 2.2 by 2.5 degrees and on distractor absent trials the centre of the screen was blank. The maximum size of a square was always 2.3 degrees and the minimum size was 0.5 degrees. There were no non-target squares; participants enumerated all white squares on screen while ignoring the cartoon distractor.

The set size and presence/ absence of a distractor stimulus were counterbalanced and trials were presented in random order such that any combination was equally likely on any given trial. After a practice block of 12 trials, participants completed four experimental blocks of 108 trials with a self-paced break in between blocks.

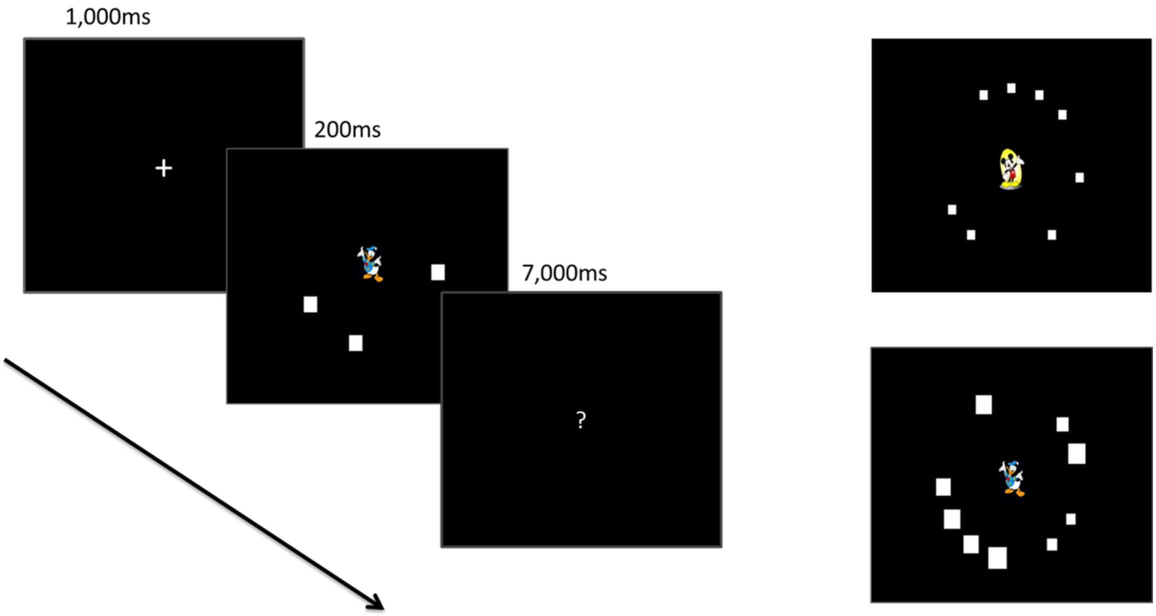

Figure 2.4 Left: A typical trial in the enumeration task of Experiment 2, participants report the number of white squares while ignoring the cartoon image which was present on one third of trials. Right: An example display from the uniform square size condition (top) and the random square size condition (bottom).

2.3.2 Results

Once again, participants were excluded from analysis if their response accuracy was below 60% correct on the lowest set size of the enumeration task on trials where no distractor was present. This led to the exclusion of 3 participants, the final sample analysed was therefore n = 85 participants, 69 of whom were female, aged 18-21 (M =18.86, SD = 0.83).

Accuracy

Average accuracy is presented as a function of set size (1-12) and distractor condition (present or absent) in Table 2.2. Accuracy was generally higher than in Experiment 1 as intended but still decreased with increasing set size beyond the subitizing range.

	Distractor absent		**Distractor present**	
Set size	**Average accuracy (% correct)**	**SD**	**Average accuracy (% correct)**	**SD**
1	98.84	3.40	98.32	4.95
2	98.32	5.42	98.19	5.84
3	97.59	4.54	97.15	7.03
4	93.08	8.70	90.28	14.98
5	79.65	15.53	80.40	19.81
6	66.91	13.60	71.26	22.60
7	56.51	15.75	60.78	20.52
8	50.68	13.89	52.36	17.45
9	42.85	12.64	45.95	17.73
10	19.61	15.46	21.88	22.37
11	20.46	15.65	20.24	22.76
12	20.28	20.67	23.64	27.10

Table 2.2 Average accuracy in the enumeration task of Experiment 2 for trials with and without distractor stimuli.

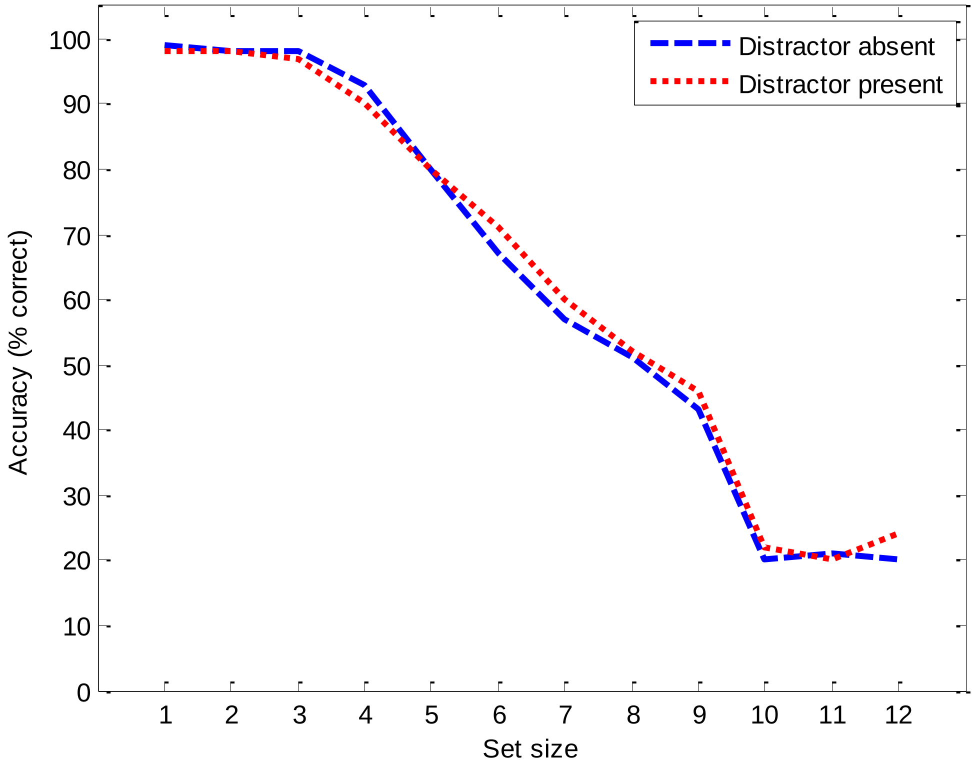

Figure 2.5 Average accuracy in the enumeration task of Experiment 2 plotted as a function of set size for trials without a distractor (blue dashed line) and trials with a distractor (red dotted line).

Accuracy scores were entered into a 2x2x12 repeated measures ANOVA with a between-subjects factor of stimulus type (equally sized squares or constant overall size) and within subjects factors of distractor (present or absent) and set size (number of squares from 1-12). There was a significant effect of set size (F(11,74) = 783.69, p< .001, η_p^2 = .99) but no significant effect of distractor condition or stimulus type and no interaction (all p's> .1). As can be seen in Table 2.2 and Figure 2.5, accuracy was relatively high (over 50%) up to set size eight, beyond which performance dropped below 50%. It appears that for the highest set sizes participants were still unable to perform the task accurately despite the changes made to the task.

Response times

The enumeration task in Experiment 2 was designed to allow analysis of response times. Average response accuracy was near chance at set sizes 9 and above, and several participants had no trials with correct responses for these set sizes, the following analyses therefore focused upon response times at set sizes 1-8 as in the analyses of accuracy in Experiment 1. Table 2.3 shows the average reaction times for trials with correct responses at each set size with distractor present and absent.

	Distractor absent		**Distractor present**	
Set size	**Average RT (ms)**	**SD**	**Average RT (ms)**	**SD**
1	820	128	922	127
2	838	118	957	128
3	842	140	986	150
4	975	152	1,085	175
5	1,156	204	1,203	214
6	1,466	340	1,496	287
7	1,667	439	1,640	492
8	1,822	504	1,783	648

Table 2.3 Average response time (in milliseconds) for each set size in the enumeration task of Experiment 2 for trials with and without distractor stimuli.

Response times were entered into a 2x2x8 repeated measures ANOVA with a between-subjects factor of stimulus type (equally sized squares or constant overall size) and within subjects factors of distractor condition (present or absent) and set size (number of squares from 1-8). There was no significant effect of stimulus type or any interaction involving stimulus type (all F's < 1.39, all p's > .1) indicating that neither absolute saturation nor individual square size was effectively used as a cue to set size.

There was a significant effect of set size (F(7,77)= 75.73, p< .001, η_p^2 = .88), indicating that reaction times were significantly slower when enumerating larger quantities. There was also a significant effect of distractor condition (F(1,83)= 30.31, p<.001, η_p^2 = .27), indicating that reaction times were significantly slower in the presence of a distractor stimulus. Importantly, there was a significant interaction between the effects of set size and distractor condition (F(7,77) = 6.24, p<.001, η_p^2 = .36). Figure 2.6 illustrates reaction times at each set size with distractors present and absent. As can be seen from the figure, reaction times are slower in the presence of a distractor but only at lower set sizes.

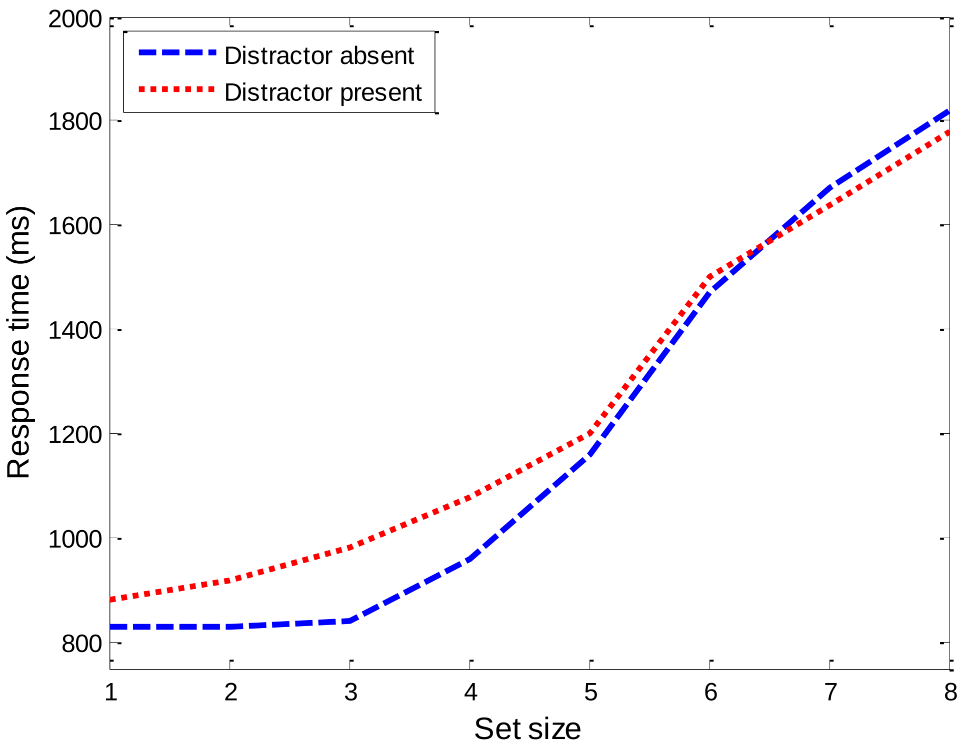

Figure 2.6 Average response time (in milliseconds) as a function of set size in the enumeration task of Experiment 2 for trials without a distractor (blue dashed line) and for trials with a distractor (red dotted line).

There was a significant difference between distractor (present and absent) conditions for set sizes one to four (Set size 1: t(84)= -11.52, p<.001; Set size 2: t(84)= -15.01, p<.001; Set size 3: t(84)= -19.45, p < .001; Set size 4: t(84)= -11.18, p<.001), all of which withstood Bonferroni correction for multiple comparisons. There was a significant difference at set size five which did not survive Bonferroni correction (t(84)= -2.61, p =.01). There was no significant effect of distractor at any higher set size (all t's < 1, all p's > .1).

Individual differences

Each participant’s subitizing capacity was estimated by fitting a bilinear function as in Experiment 1, this time to the response time data. The first linear component was fit with starting values of 0ms and 800ms for the slope and intercept respectively, the second linear component was fit with a starting value of 100ms for the slope. Once again the bilinear function fit the data well, average RMSE was 70.30ms (SD = 37.83), average adjusted R^2= .92 (SD = .07). The average estimated capacity limit across the entire sample was 3.12 (SD = 0.72, range: 1.1 – 5.8). As in Experiment 1, the sample was split into upper and lower quartiles based on their subitizing capacity. The average subitizing range was 2.29 (SD = 0.41, range: 1.1 – 2.6) for the lower capacity quartile and 4.01 (SD = 0.56, range: 3.5 – 5.8) for the high capacity quartile.

As in Experiment 1, higher capacity individuals were expected to remain prone to distraction at relatively higher set sizes than lower capacity individuals, for whom capacity should be exhausted by a more moderate increase in set size. To investigate this, the upper and lower capacity quartiles were compared as in Experiment 1. Distractor cost scores for the low and high capacity quartiles were entered into a 2x2 ANOVA with set size (low: 1-2 items; high: 3-4 items) as a within subjects factor and quartile group (high vs. low) as a between subjects factor. The main effect of set size was significant (F(1,41)= 5.67, p< .05) and there was a significant interaction between load and quartile group (F(1,41)= 4.51, p<.05).

Follow-up t-tests revealed that there was a significant effect of increased set size for the low capacity group (t(20)= 5.47, p<.05) but not for the high capacity group (p>.05). As in Experiment 1, distractor interference was significantly reduced by the moderate increase in load for low capacity participants but not for those with greater capacity.

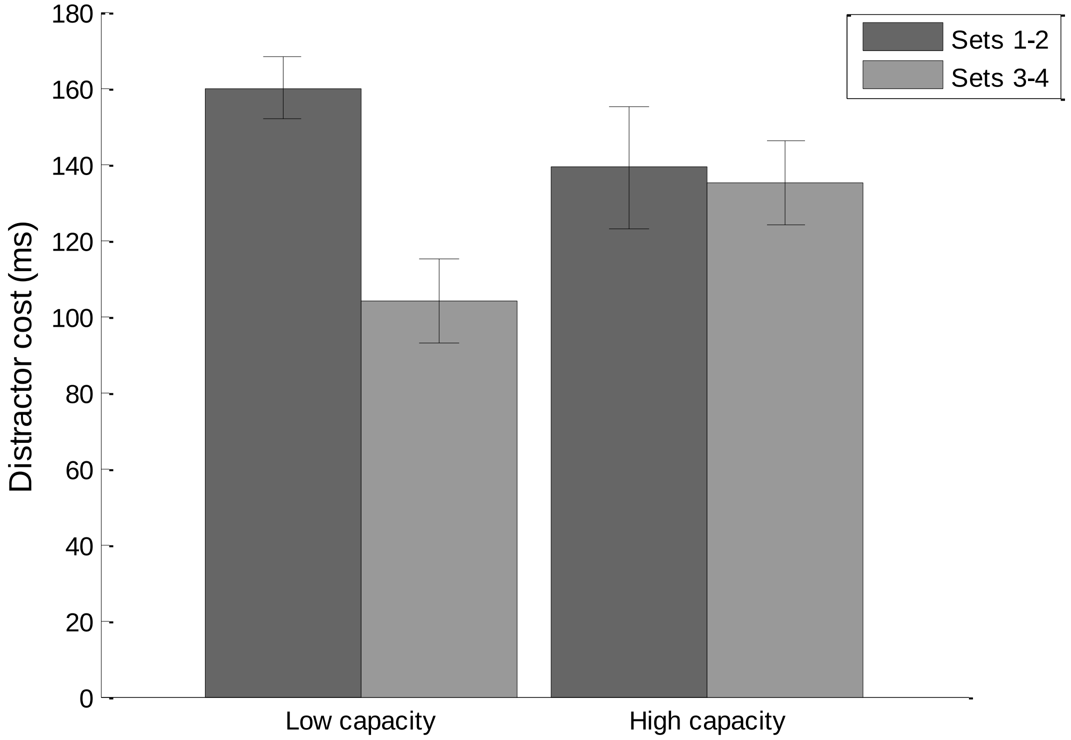

Figure 2.7 A bar graph for the comparison of high- and low-capacity quartiles in terms of distractor cost averaged over sets one-two and sets three-four in Experiment 2.

2.3.3 Conclusions

As in Experiment 1, participants' performance was significantly worse in the presence of a distractor but this effect was only observed within the subitizing range. Once again, distractor interference was significantly reduced by a relatively (compared to Experiment 1) small increase in set size for participants with lower capacity, but there was no significant reduction for higher capacity participants. The results of Experiment 2 are unlikely to be attributed to participants adopting a 'guessing' strategy for set sizes beyond their subitizing range as accuracy remained relatively high far beyond typical capacity limits but still the influence of distractors depended on their subitizing capacity.

2.4 Chapter conclusions

The experiments in this chapter demonstrate for the first time that attention capture by irrelevant distractors during visual enumeration is dependent upon the subitizing range. In both experiments participants' only task was to report the number of stimuli presented in a ring around fixation while ignoring central distractor images. The results of both experiments demonstrated that participants were unable to suppress distractor processing during subitizing and that distraction was eliminated when the subitizing range was surpassed. Furthermore, in both experiments, individual differences in subitizing capacity were shown to play a significant role in determining distraction. For the lowest capacity participants, distractor processing was eliminated by an increase from set sizes one and two to set sizes three and four; whereas the highest capacity participants showed no significant reduction.

These results are in line with the predictions of load theory, which states that distractors will automatically be selected provided there is perceptual capacity available to process them. Despite there being several parallels between the visual enumeration and load theory literatures, until now there has been very limited research directly connecting the two fields. While previous research established that perceptual load on a concurrent task interferes with subitizing performance (Vetter et al. 2008; Burr et al. 2010), these findings were limited to dual-task paradigms. As previous studies used dual-task paradigms, in which participants were instructed to attend to a central task of low or high load, it was impossible to establish the automaticity of perceptual processing during enumeration. The present results establish that distractor processing is automatic within the subitizing range, in line with the predictions of load theory. This effect is most likely attributable to spill-over of perceptual resources as executive control was not loaded by dual-task demands (Boot et al. 2005; De Fockert, 2013).

Taken together with previous literature, these results provide compelling evidence that the subitizing phenomenon represents the domain general perceptual capacity described in load theory. Furthermore, these findings support the hypothesis that individuals differ in their perceptual resources, as suggested by previous research on special populations (see General Introduction section 1.2.4). This has intriguing implications for individual differences research in the load theory literature, a topic which has previously received only limited attention.

Chapter 3

Subitizing capacity as a predictor of subjective awareness

3.1 Chapter introduction

The results of Chapter 2 established a link between subitizing capacity and distractor interference in a visual enumeration task, suggesting that subitizing draws on perceptual capacity. In both experiments, enumeration performance was significantly affected by the presence of a distractor stimulus, but only up to a set size of four items (i.e. within the subitizing range). Furthermore, distractor interference was also subject to individual differences in subitizing capacity. For participants who could only subitize one or two items the influence of distractors was eliminated by sets of more than two, whereas for participants with greater subitizing capacities the influence of distractors was still present up to sets of four targets.

This is in accordance with the predictions of load theory, in which perceptual capacity is thought to spill-over to unattended stimuli, leading to distraction, unless capacity is exhausted by the task. The results of Chapter 2 therefore provide preliminary support for the hypothesis that a general perceptual capacity underlies subitizing and that individual differences in subitizing capacity can determine unattended perception. However, as no report of awareness was assessed for distractor stimuli it is impossible to make any conclusion regarding participants’ awareness of the stimulus.

My aim in this chapter was to investigate the degree to which individual differences in perceptual capacity determine awareness in a task-general sense, using subjective blindness paradigms and relating them to a visual enumeration task. I will therefore briefly revisit literature regarding inattentional blindness phenomena described in the General Introduction and the role of perceptual load in determining subjective awareness in these paradigms.

In a famous demonstration of inattentional blindness, Simons and Chabris (1999) found that when counting the number of times a basketball was passed between players in a video, many observers failed to notice the appearance of an additional person dressed in a gorilla suit walking through the scene. The number of observers who noticed the gorilla was reduced even further when they were instructed to keep separate counts for two different types of ball pass (bounces or throws). This is an early demonstration of the role of perceptual load in inattentional blindness, increased perceptual load (attending two types of perceptual event rather than one) lead to increased rates of inattentional blindness. Cartwright-Finch and Lavie (2007) further confirmed the role of perceptual load in determining inattentional blindness by measuring awareness for an unexpected critical stimulus during a task of either low or high perceptual load. With two different manipulations (see General Introduction, section 1.2.1) they found that high load lead to significantly increased rates of inattentional blindness.

Macdonald and Lavie (2008) aimed to determine the role of perceptual load in stimulus detection using a modification of this design. In their ‘Load-induced blindness’ paradigm, participants were instructed to perform a central task which involved either low or high perceptual load while also attempting to detect the occasional presence of a peripheral stimulus. This allowed for analysis of stimulus detection sensitivity rather than being limited to the binary ‘blind’ or ‘not blind’ measure provided by traditional inattentional blindness tasks. The results of this investigation and several subsequent studies demonstrated that high perceptual load lead to significantly reduced detection sensitivity for the peripheral targets. Similarly, detection of changes in the change blindness flicker paradigm has been shown to be significantly impaired by high perceptual load in a concurrent visual search task (Beck et al. 2001).

Collectively, these results demonstrate that subjective awareness of a stimulus depends upon perceptual load in the same way as distractor processing. This therefore implies that perceptual capacity should apply generally to situations in which the observer attempts to detect a stimulus. In Chapter 3 I tested this hypothesis by investigating whether subitizing capacity is a significant predictor of stimulus detection in the load-induced blindness and change blindness paradigms. Participants in two experiments performed a visual enumeration task in which they reported the number of stimuli presented briefly onscreen with no secondary task demands and no distractor stimuli. Subitizing capacity was measured for each participant as the point at which their response accuracy began to decrease with increasing set size. In each experiment, participants also completed either a change blindness task (Experiment 3) or a load-induced blindness task (Experiment 4). The hypothesis that a general perceptual capacity underlies subitizing and stimulus detection in these paradigms leads to the prediction that they will share unique variance which cannot be accounted for by general effort or other cognitive constructs. The ability to estimate larger sets (which are beyond the subitizing range) was used as a measure of performance factors not specific to perceptual capacity and was therefore predicted not to have a specific relationship with detection beyond that shared by subitizing capacity.

3.2 Experiment 3

Participants performed a visual enumeration task in which they were required to rapidly report the number squares from a brief and masked presentation. As in Chapter 2 (Experiment 1) their subitizing capacity was taken as the point at which the report-accuracy/ set-size function transitioned from a flat to a negative slope. Visual detection was measured using a change blindness ‘flicker task’ (Rensink, O’Reagan & Clark, 1997) in which participants attempted to detect changes in a rapidly flickering real world scene.

The hypothesis that both subitizing and visual awareness depend upon a common perceptual capacity limit led me to the prediction that there would be a positive association between subitizing capacity and the ability to detect changes. Furthermore, this association should not be accounted for by performance factors other than perceptual capacity.

3.2.1 Method

Participants

Participants were public volunteers in the ‘Live Science’ exhibition at the Science Museum in London. A total of n = 296 participants (132 male), aged 18 to 64 (*Mean* = 31.33, SD = 13.34) completed Experiment 3.

Stimuli and procedure

All participants provided written informed consent prior to participation and reported normal or corrected-to-normal vision. The experiment was conducted in a quiet section of the museum which was screened from the museum floor. The testing area contained three computers and participants completed the experiment in groups of one to three. The task was explained to each participant individually and there was always at least one researcher present throughout the experiment. Experimental tasks were presented with Matlab (Mathworks, Inc., Natick, MA) using the Cogent toolbox (www.vislab.ucl.ac.uk/cogent.php). Participants were seated approximately 60cm from the screen, however as a constant distance cannot be guaranteed stimulus sizes are reported in cm.

Enumeration task

Each enumeration trial (Figure 3.1) began with a fixation point for 1s; following this a set of black squares was presented for 100ms. This was followed immediately by a central noise mask made up of randomly positioned black and white squares covering the same area as the stimulus display (7.5cm by 7.5cm). After 400ms the mask was replaced by a central ‘?’ response prompt which remained onscreen for 2,400ms or until a response was made. The squares were randomly positioned in an area subtending 7.5cm by 7.5cm in the centre of the screen. The squares varied in size, ranging from a minimum of 0.4 to a maximum of 4cm in diameter. Participants were instructed to respond as quickly as possible indicating the number of squares displayed by pressing a key from 1-9 on the right-hand number pad of the keyboard. They could respond at any time following the initial stimulus display.

The task comprised of one practice block of 6 trials, followed by three experimental blocks of 54 trials (18 trials of each set size). After the task was explained to them, participants completed the practice block and confirmed that they understood the instructions before continuing to the experimental trials.

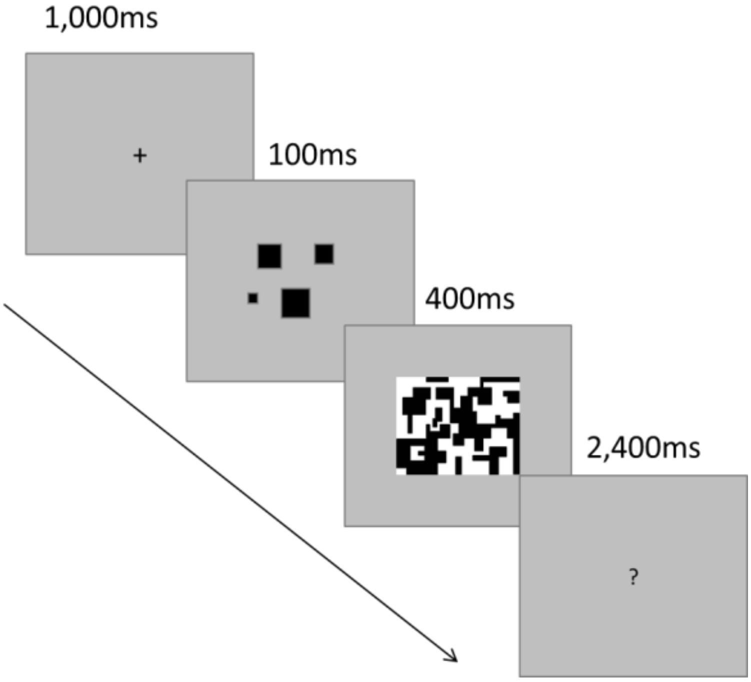

Figure 3.1 Schematic of the enumeration task used in both Experiments 3 and 4.

Change blindness task

Each trial began with a fixation point for 1 second, which was followed by the presentation of a photograph of an outdoor scene (22.5cm by 13.52cm). The image was presented for 200ms, followed by a grey rectangle of matching dimensions for 100ms and then by a second image for a further 200ms, which was again replaced by a grey rectangle presented for 100ms (Figure 3.2). The stimuli cycled repeatedly in this fashion for a maximum of 15s or until participants responded. After a response was made, a green tick (3.1cm by 3.82cm) or a red cross (2.5cm by 2.5cm) appeared onscreen for 700ms indicating that the response was correct or incorrect respectively.

The scene stimuli could either be identical (50% of trials) or could contain a slight but conspicuous change (50% of trials). Participants were instructed to respond by pressing the right shift key on the computer keyboard if a change was present or the left shift key if there was no change. They were instructed to respond as soon as they thought they knew the answer, if the 15 seconds expired with no response being made a ‘no-change’ response was recorded. The task consisted of 44 trials, each of which was initiated by the participant by pressing the space bar when they were ready. After the task was explained to them, participants completed one demonstration practice and then commenced the experimental trials.

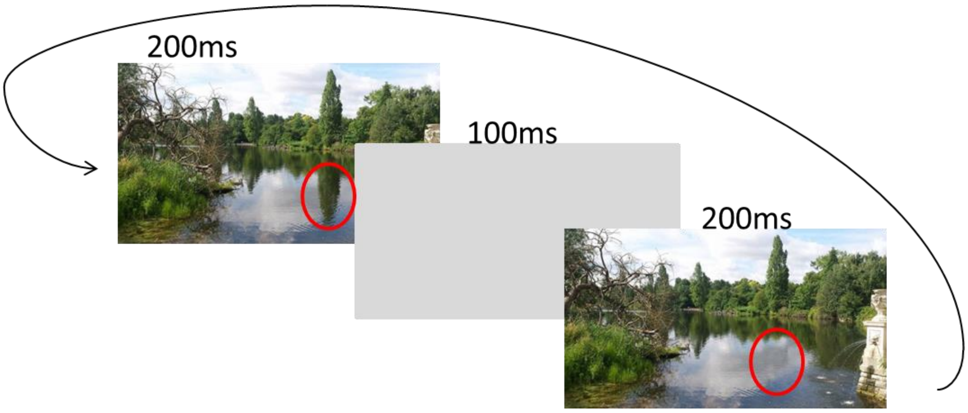

Figure 3.2 Schematic of the change blindness task used in Experiment 3.

3.2.2 Results

Participants' data were excluded from analysis if their accuracy was below 60% in the lowest set size of the enumeration task (11 participants), or if their false alarm rate exceeded two standard deviations of the group average in the change blindness task (8 participants). The final sample therefore included n = 277 participants (127 male), aged 18 to 64 (*Mean* = 30.40 SD = 12.07).

Enumeration task performance

A curve fitting procedure was used as in the individual differences analyses of Chapter 1 to establish the subitizing capacity for each participant based on their enumeration accuracy at each set size from one to eight (as in Experiment 1). The average fit of the function to the enumeration data was good: the average RMSE was 8.02% (SD = 4.39) and average adjusted R^2 value was 0.78 (SD = .20). Thus the function appears to predict observed scores well. The average subitizing capacity estimate was 3.63 (SD = 0.92). To obtain a measure of performance not dependent upon subitizing, 'Estimation' accuracy for higher set sizes was calculated by averaging the accuracy at all set sizes above the performance breakpoint for each participant. Average estimation accuracy was 46.02% (SD = 10.91).

Change blindness task performance

Average performance in the change blindness task is presented in Table 3.1. False alarm rate was very low (as is typical of change blindness paradigms) and so a nonparametric estimate of detection sensitivity (A) was calculated using the formula described by Zhang & Mueller (2005) along with the associated measure of decision bias (b).

	Mean	SD
Detection rate	.68	.13
False alarm rate	.44	.62
Sensitivity (A)	.89	.06
Bias (b)	1.99	0.49

Table 3.1 Average detection rates, false alarm rates, detection sensitivity (A) and decision bias (b) for the change blindness task of Experiment 3.

Detection rate

Subitizing capacity was significantly correlated with detection rate in the change blindness task (r(276) = .32, p < .001): Individuals who subitized more items detected more changes. There was also a weaker correlation between detection rate and estimation accuracy (r(276) = .16, p < .005).

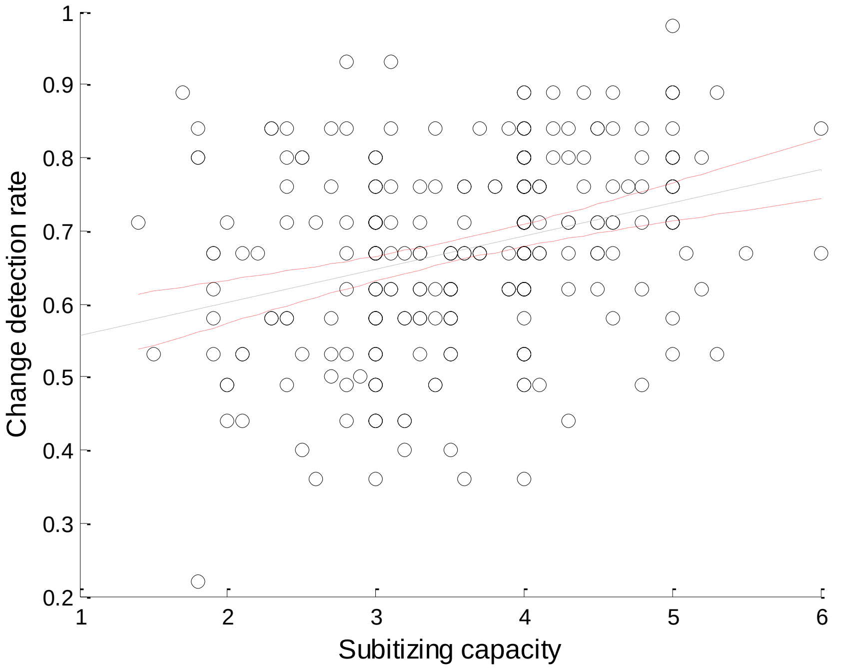

Figure 3.3 Scatterplot of the correlation between change blindness detection rate and subitizing capacity (red dashed lines represent 95% confidence intervals).

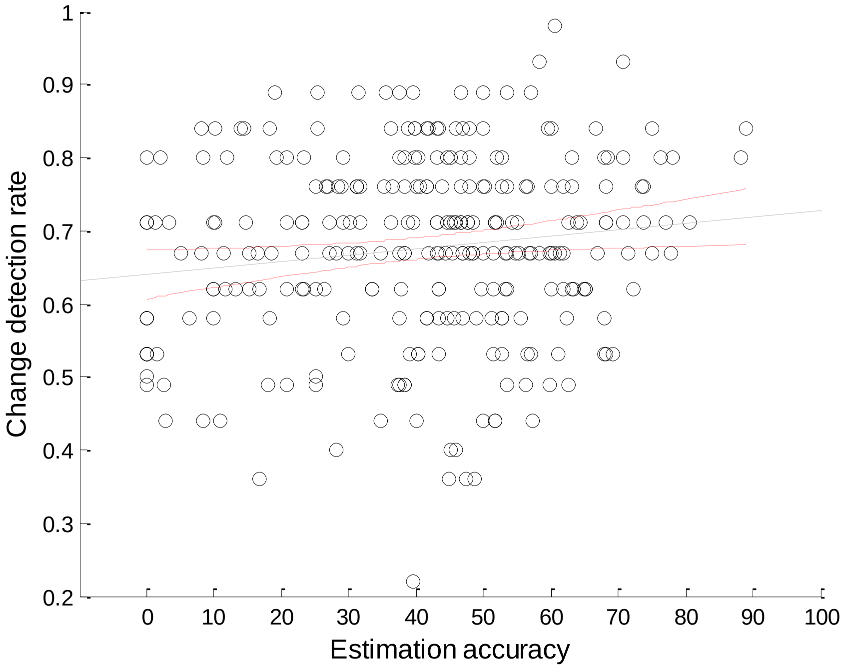

Figure 3.4 Scatterplot of the correlation between change blindness detection rate and estimation accuracy (red dashed lines represent 95% confidence intervals).

The unique contributions of both subitizing and estimation to change detection were analysed in a multiple regression. Subitizing and estimation were entered simultaneously in a single model. The regression was significant ($R^2 = .15$, $p < .001$) and both subitizing capacity and estimation accuracy accounted for significant unique variance (Table 3.2).

Model	**Predictor**	**Beta**	**t**	**Sig**
1	Constant		11.567	<.001
$R^2= .15$	Estimation	.237	4.121	<.001
p< .001	Subitizing	.364	6.347	<.001

Table 3.2 Results of a multiple regression predicting change blindness detection rates from subitizing and estimation.

Detection sensitivity

In order to establish that these results are not explained by reduced susceptibility to false alarms or response bias, the analyses were replicated using change detection sensitivity (A; Zhang & Mueller, 2005) in place of detection rate. Detection sensitivity in the change blindness task was positively correlated with subitizing capacity (r(276) = .39, $p < .001$), decision criterion (b) was not (r(276) = -.08, $p > .05$). Again, there was also a weaker positive correlation between change detection sensitivity and average estimation accuracy (r(276) = .15, $p < .05$).

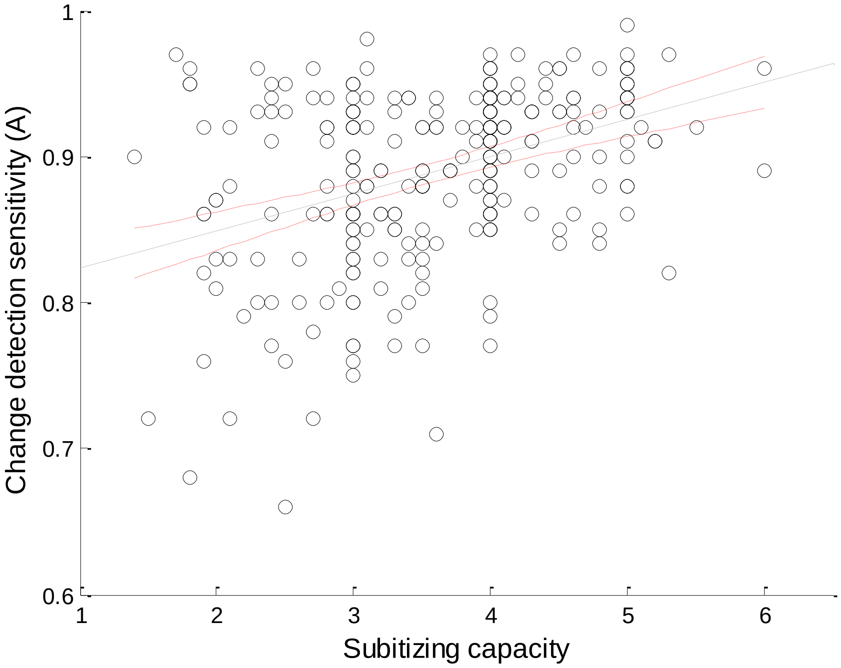

Figure 3.5 Scatterplot of the correlation between change blindness detection sensitivity and subitizing capacity (red dashed lines indicate 95% confidence intervals).

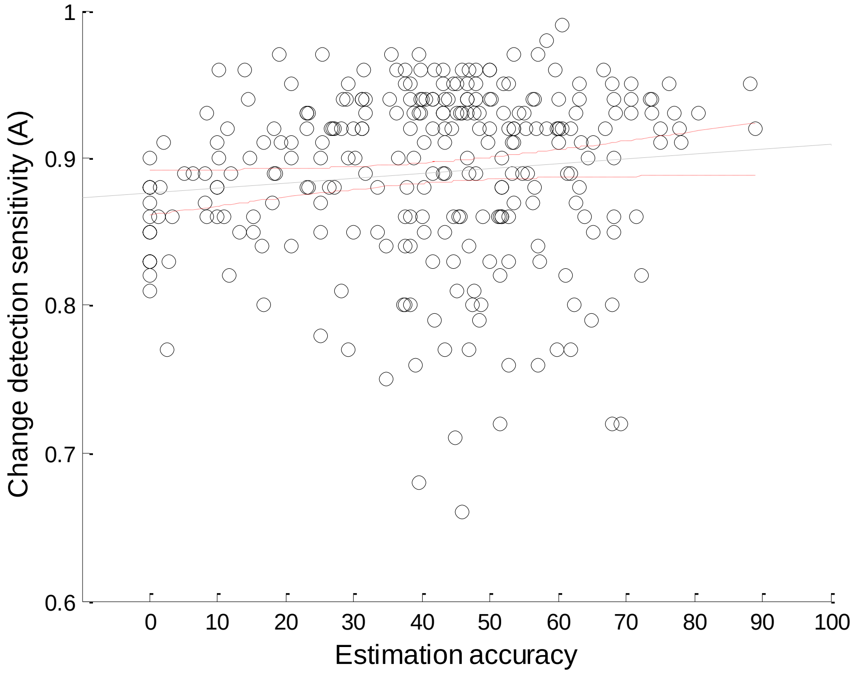

Figure 3.6 Scatterplot of the correlation between change blindness detection sensitivity and estimation accuracy (red dashed lines represent 95% confidence intervals).

As previously, these relationships were further examined with a multiple regression which included the same variables as in the analysis of detection rate, this time predicting detection sensitivity. The regression was significant ($R^2 = .19$, $p < .001$) and once again both subitizing capacity and estimation accuracy accounted for a significant unique variance (Table 3.3).

Model	**Predictor**	**Beta**	**t**	**Sig**
1	Constant		47.155	<.001
$R^2 = .19$	Estimation	.254	4.553	<.001
$p < .001$	Subitizing	.431	7.743	<.001

Table 3.3 Results of a multiple regression predicting change blindness detection sensitivity from subitizing and estimation.

3.2.3 Conclusions

These results support the hypothesis that subitizing and change detection depend upon a common underlying capacity. The observed relationship is unlikely to be explained by general factors (e.g. motivation) as there was significant unique variance when estimation accuracy was included as a covariate in multiple regression analyses. Estimation of larger sets is thought to reflect a separate cognitive process to subitizing (e.g. Burr & Ross, 2010; Cutini & Bonato, 2012; Vetter et al. 2011) but should have been similarly affected by general factors as within and supra-capacity sets were randomly intermixed and involved very similar displays. The unique variance associated with subitizing when including estimation accuracy as a covariate suggests subitizing is a specific predictor of awareness. Furthermore, these results hold true when analysing either detection rates or detection sensitivity, indicating that the common variance is associated with capacity for visual detection of stimuli rather than a reduced susceptibility to false alarms or a change in response bias.

The change blindness flicker task is regularly used to demonstrate limitations of perception and attention (e.g. Ambinder & Simons, 2005). However, the sequential nature of the ‘flickering’ stimulus display and the extended trial duration (over several seconds) may mean that alternative cognitive capacities such as working memory storage or executive control may play a significant role. This may explain the significant unique association with estimation accuracy.

3.3 Experiment 4

The aim of Experiment 4 was to further establish that perceptual capacity is a key determinant of visual awareness and to clarify the nature of perceptual capacity limits. Subitizing capacity was thus used as a predictor of awareness once more, this time in a ‘load-induced blindness’ task (Macdonald & Lavie, 2008). In this task, participants attempted to detect the occasional presence of peripheral target stimuli while also engaged in an attention-demanding task requiring judgement of the relative arm lengths of a simultaneously presented central cross. I predicted that (as in Experiment 3) individuals who subitized more items would detect stimuli with greater sensitivity, and that this effect would not be explained by performance factors outside subitizing capacity.

3.3.1 Method

Participants

Once again, participants were members of the public who volunteered to take part as part of the 'Live Science' exhibition at the Science Museum. 165 participants (80 male), aged 18 to 62 (*Mean* = 26.56, SD = 9.75) completed the experiment.

Stimuli and procedure

Participants were tested in the same conditions as Experiment 3, in groups of one to three; they completed the same visual enumeration task as described in Experiment 3. Instead of the change blindness flicker task, this time participants also completed a load-induced blindness task.

Load-induced blindness task

Each trial began with a central fixation dot for 1 second which was followed by a central cross and four peripheral black and white gratings for 120ms. After this a blank (response) screen was presented for 1880ms, followed by a central '?' prompt for 100ms and then another blank screen for a further 1900ms (Figure 3.7). The cross was formed of one vertical and one horizontal line, one of which was always longer (4.5cm) than the other (3.5cm). The vertical arm was longer on a random 50% of trials and on remaining trials the horizontal arm was longer. The gratings (3.6cm x 3.6cm) appeared in each corner of the screen, with 6.4cm distance from the nearest corner of the grating to the centre of the screen (and cross). The contrast of the (non-target) gratings was 10%; on 25% of trials the contrast of one (target) grating was incremented by an additional 28%.

Participants were instructed to respond immediately after the stimulus presentation by pressing either the 'up' or the 'left' arrow key to indicate which arm of the cross (vertical or horizontal) was longer. They were then instructed to indicate after the ‘?’ prompt whether any of the four gratings was brighter by pressing the spacebar.

Participants completed 10 practice trials, followed by two experimental blocks of 32 trials and finally one control block of 32 trials. After receiving instructions, they completed the practice trials and confirmed that they understood the task and then completed the experimental blocks. After this they received revised instructions for the control trials. Control trials were identical to the experimental trials except that participants were instructed not to attend to the arm length discrimination. The ‘?’ prompt immediately followed the stimulus display and participants indicated whether one of the gratings was brighter as in experimental trials. Participants were instructed to maintain fixation throughout the task and were advised that any grating had an equal chance of being a target.

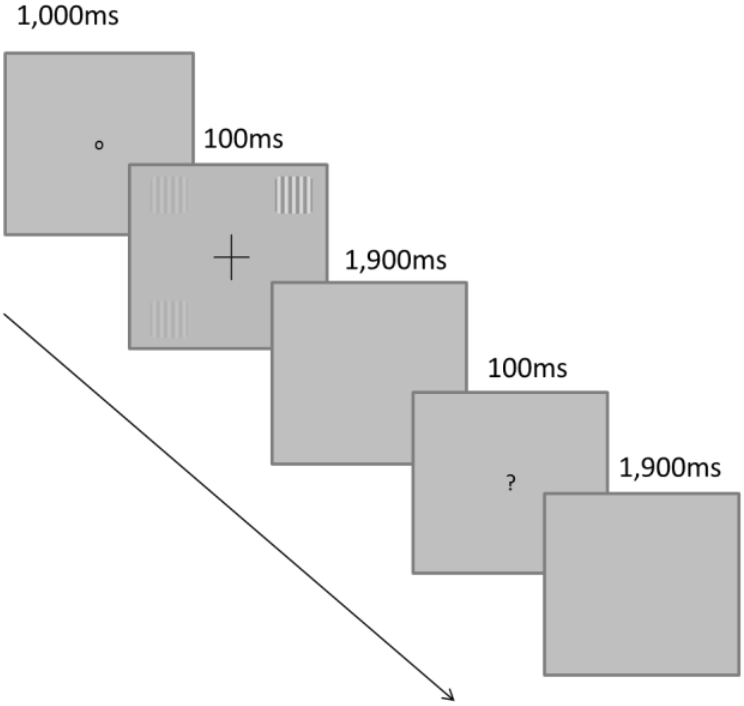

Figure 3.7 Schematic of the load-induced blindness task used in Experiment 4.

3.3.2 Results

Participants' data were excluded from analysis if their accuracy was below 60% in the lowest set size of the enumeration task (10 participants), if their detection sensitivity was more than two standard deviations below the group average in the control block of the load-induced blindness task (13 participants) or if their accuracy in the central cross arm judgement was near chance (below 60% correct) in the main block of the load-induced blindness task (20 participants). The final sample analysed was therefore n = 122 (59 male) aged 18 to 62 (*Mean* = 25.22, SD = 8.89).

Load-induced blindness task performance

Average performance in the contrast detection task is presented in Table 3.4. Detection sensitivity (A) and response criterion (b) were calculated using the same measures as in Experiment 3.

	Mean	**SD**
Detection rate	.70	.21
False alarm rate	.24	.18
Sensitivity (A)	.80	.12
Bias (b)	1.16	0.55

Table 3.4 Average detection rates, false alarm rates, detection sensitivity (A) and decision bias (b) for the load-induced blindness task of Experiment 4.

Enumeration task

Subitizing capacity was estimated as in Experiments 1 and 3 by fitting a bilinear function to each individual's accuracy data at each set size (excluding set size nine). The fit of the function to the data was similar to previous experiments (Average RMSE = 8.10, SD = 4.40; average R-squared = .77, SD = .20). The average capacity estimate was 3.32 (SD = 0.83) and average estimation accuracy was 51.03% (SD = 11.01).

Detection rate

Subitizing capacity was positively correlated with detection rate in the load-induced blindness task (r(121) = .29, p < .001), as was estimation accuracy (r(121) = .22, p <.05).

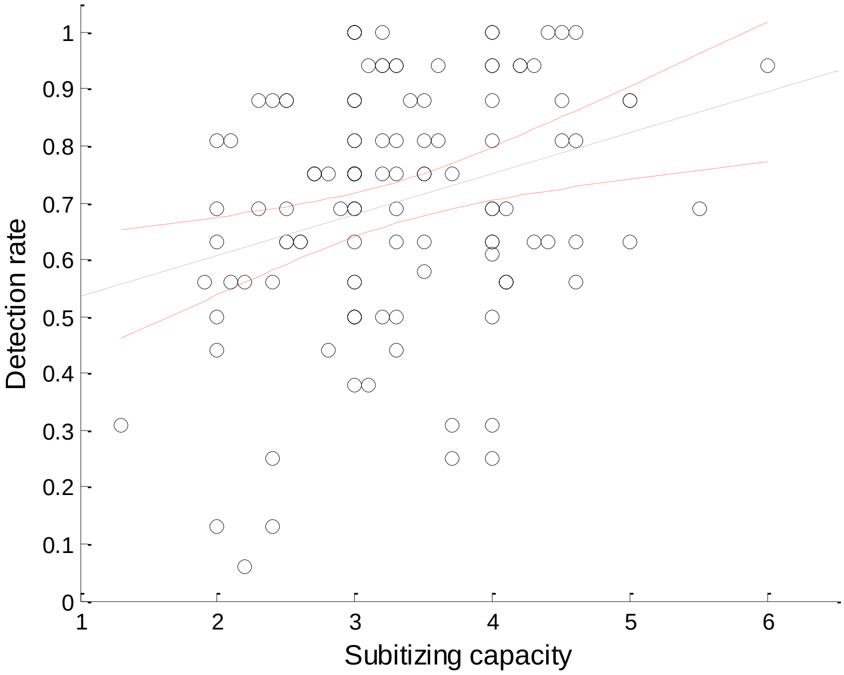

Figure 3.8 Scatterplot of the correlation between load-induced blindness detection rate and subitizing capacity (red dashed lines represent 95% confidence intervals).

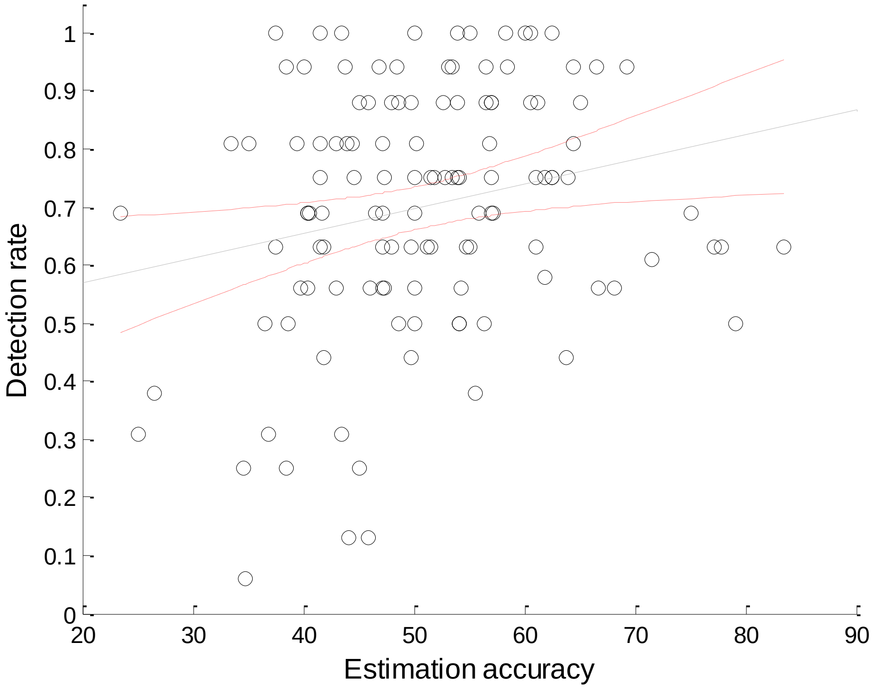

Figure 3.9 Scatterplot of the correlation between load-induced blindness detection rate and estimation accuracy (red dashed lines represent 95% confidence intervals).

As in Experiment 3, a multiple regression was used to determine the unique contributions of subitizing and estimation; which were entered simultaneously as predictors of detection rate. The regression was significant (R^2= .09, p < .005), subitizing capacity accounted for a significant portion of unique variance while estimation accuracy did not (Table 3.5). As previously, variance associated with general factors such as motivation are expected to have a similar effect on both subitizing and estimation.

Model	Predictor	Beta	t	Sig
1	Constant		3.426	.001
R^2= .09	Estimation	.157	1.746	.083
P< .005	Subitizing	.244	2.704	.008

Table 3.5 Results of a multiple regression predicting load-induced blindness detection rate from subitizing and estimation.

Detection sensitivity

Detection sensitivity and subitizing capacity were positively correlated (r(121) = .38, p < .001), detection decision criterion (b) was not (r(121) = .08, p > .05). Estimation accuracy (r(121) = .25, p < .01) was also correlated with detection sensitivity.

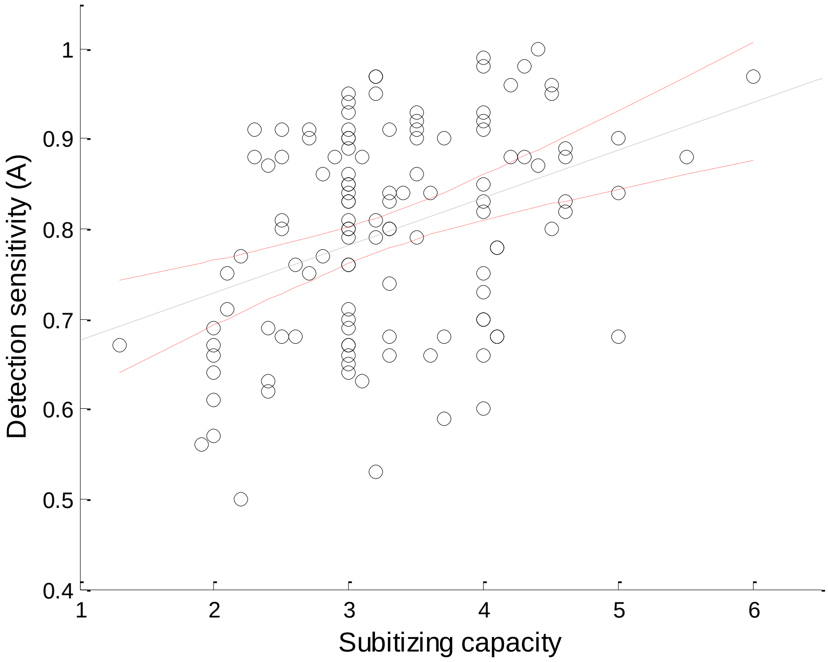

Figure 3.10 Scatterplot of the correlation between load-induced blindness detection sensitivity and subitizing capacity (red dashed lines represent 95% confidence intervals).

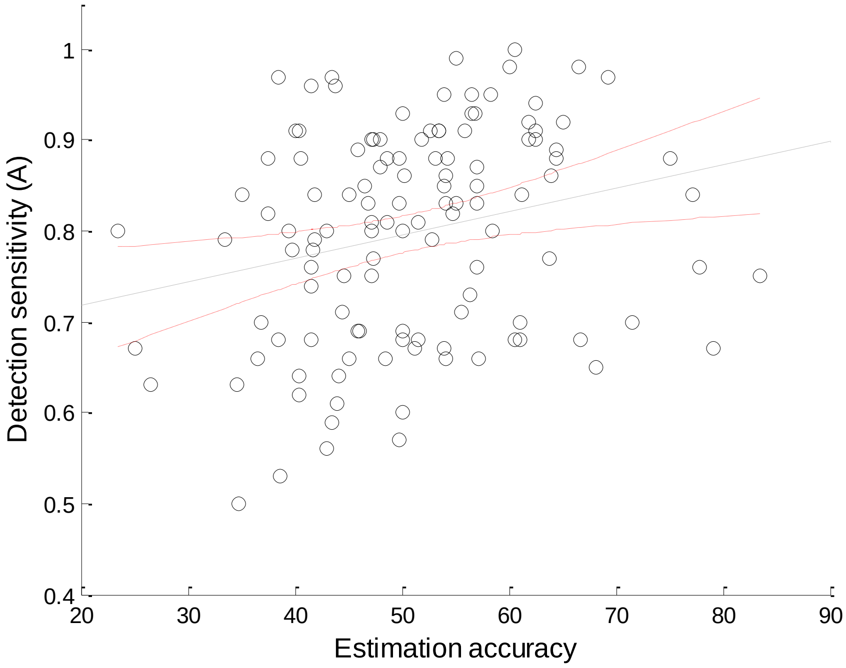

Figure 3.11 Scatterplot of the correlation between load-induced blindness detection sensitivity and estimation accuracy (red dashed lines represent 95% confidence intervals).

Once again, the inter-relations of the three variables were analysed in a multiple regression, this time predicting detection sensitivity (A). As in the previous analysis the regression was significant ($R^2 = .15$, $p < .001$) and subitizing capacity accounted for the only significant unique variance (Table 3.6). Thus after controlling for any common variance shared by both subitizing and estimation, only subitizing is a significant predictor of detection sensitivity, replicating the previous results.

Model	**Predictor**	**Beta**	**t**	**Sig**
1	Constant		10.428	<.001
$R^2 = .15$	Estimation	.154	1.768	.080
P< .001	Subitizing	.339	3.894	<.001

Table 3.6 Results of a multiple regression predicting load-induced blindness detection sensitivity from subitizing and estimation.

3.4 Chapter conclusions

The results of these experiments support the conclusion that a common perceptual capacity limit underlies individual differences in subitizing and visual awareness. In both experiments, subitizing was a unique predictor of awareness when controlling for estimation accuracy and in Experiment 4 it was the only unique factor (despite estimation accuracy being significantly correlated with stimulus detection).

The enumeration task used in both experiments involved displays within and beyond the subitizing range randomly intermixed. The rapid and masked displays did not provide sufficient time to flexibly adopt a different encoding strategy for displays which can and cannot be subitized (i.e. serial counting was not possible). Any anticipatory, motivational or alternative cognitive resources applied to the task are therefore likely to be common to both the subitizing and estimation performance measures; the only distinguishing factor being that they were within or beyond perceptual capacity.

The subjective blindness paradigms have both historically been used to establish the necessity of attentional resources for conscious perception. This common factor coupled with their distinctive perceptual requirements makes them mutually complementary as tests of common perceptual capacity limits. The change blindness flicker paradigm involves repeated presentations of complex real-world scenes over several seconds. On the other hand the load-induced blindness paradigm involves dividing attention between two concurrent tasks and across multiple stimuli for a single, brief presentation. The existence of common variance shared by both of these tasks and subitizing capacity demonstrates the generality of perceptual capacity limits and its independence from superficial task details, as predicted by load theory. These results therefore support the conclusion that a task-general perceptual resource underlies awareness in these diverse paradigms.

The dissociation between the change blindness and load-induced blindness tasks in terms of their relationship with estimation accuracy demonstrates that the two tasks involve contrasting cognitive demands in addition to perceptual load. It is possible that the association between large set size estimation and change detection may be related to working memory resources, which could be involved in numerical estimation processes and in coordinated search among complex scenes. Alternatively this relationship may be related to the ability to extract the ‘gist’ or statistical summary of a visual display (e.g. Alvarez & Oliva, 2008). Outside of focused attention, the numerical gist of large quantities or the gist of a real world scene may depend upon the same cognitive process (Ward, Bear & Scholl, 2016). Whereas the specific pre-defined stimulus detection involved in the load-induced blindness task may depend on a more precise level of representation that can only be obtained within perceptual capacity. This would account for the selective association with subitizing capacity versus estimation of larger sets.

Chapter 4

Dissociable correlates of perceptual and working memory capacities

4.1 Chapter introduction

The experiments presented in Chapter 3 established common variance between subitizing and subjective blindness phenomena. This common variance remained significant when controlling for estimation accuracy, indicating that the underlying resource is specific to subitizing and cannot be explained by general performance factors. Thus, a capacity-limited perceptual resource appears to underlie awareness in these paradigms, as predicted by the load theory of attention. As discussed extensively in the General Introduction (section 1.2.2) in load theory, perceptual capacity is thought to be distinct from top-down cognitive control by working memory. Cognitive control load has been reliably established to have opposite effects to those of perceptual load, leading to increased distraction and stimulus detection (e.g. Lavie et al. 2004; De Fockert, 2013).

Thus, in Chapter 4 I sought to further investigate the role of individual differences in perceptual capacity while also accounting for executive working memory. Load theory predicts that common variance between tasks attributed to perceptual capacity should be independent to any variance associated with executive working memory resources. Although working memory capacity has been established to contribute to performance in a wide variety of tasks, any contribution is not predicted to impact the role of perceptual capacity. Alternatively, if the common variance previously attributed to perceptual capacity in Chapter 3 is actually related to cognitive control resources then there should be no unique relationship between perceptual tasks after controlling for working memory capacity.

Some recent research has investigated the role of working memory in subjective blindness phenomena. For example De Fockert and Bremner (2011) found that concurrent working memory load led to significantly increased rates of awareness in an inattentional blindness paradigm. That is, when holding in memory a more complex string of digits during the task, participants were more likely to notice unexpected peripheral stimuli. Thus, as predicted by load theory, working memory load lead to reduced rates of inattentional blindness, the opposite effect to perceptual load (as established by Cartwright-Finch & Lavie, 2007 and others).

Investigations employing an individual differences approach have had mixed results regarding the relationship between awareness and working memory. In a study by Pringle et al. (2001), working memory capacity was correlated with change blindness performance but did not account for any unique variance after accounting for VSTM capacity. A recent study by Kreitz, Furley, Memmert and Simons, (2015) failed to find any reliably significant relationship between working memory capacity and rates of inattentional blindness. However, other authors have reported contradictory results to these. For example Hannon and Richards (2010) found that individuals with greater working memory span were more likely to notice critical stimuli in a sustained inattentional blindness task (see also Richards, Hannon & Derakshan, 2010). A similar result was demonstrated by Seegmiller, Watson and Strayer (2011) who found that higher working memory capacity was associated with increased rates of noticing in the classic ‘invisible gorilla’ demonstration.

These contradictory findings may be explained by the paradigms employed in the respective studies. The studies reported by Hannon and colleagues both utilized the ‘sustained inattentional blindness paradigm’ (Most et al. 2000), which involves tracking the movements of several stimuli and counting the number of times they ‘bounce’ from the edges of the screen. This task inevitably requires working memory resources in sustaining attention over an extended trial period while simultaneously keeping a running count of ‘bounces’. The investigation presented by Seegmiller et al. (2011) assessed inattentional blindness with the ‘invisible gorilla’ video, presented to a group of students in a classroom setting. As in the sustained inattentional blindness paradigm, this assessment involves tracking for an extended period and keeping a running count of events. As working memory was directly involved in performance of the task it is not surprising that individual differences in working memory capacity played a role. However this role may not be due to awareness requiring cognitive control, instead they may merely suggest that tasks which involve working memory demands will depend on working memory abilities.

An additional aim of Chapter 4 was to further test the general nature of perceptual capacity; to this end Experiment 5 also included a motion tracking task. The paradigms employed in Chapter 3 involved very distinct stimuli and task demands, but all three tasks measured perception from very brief, transient displays. In contrast, in the MOT task several targets must be tracked simultaneously as they move among distractors for several seconds. If perceptual capacity is truly task general then MOT performance should also depend upon this capacity despite its different demands. As discussed in the General Introduction, the MOT task has previously been shown to share resources with subitizing and VSTM and has been associated with similar brain activity (e.g. Chesney & Haladjian, 2012; Fougnie & Marois, 2006; Drew & Vogel, 2008). Thus, MOT is predicted to share unique variance with the subitizing and change blindness paradigms independently from any influence of working memory capacity.

In order to investigate the role of working memory capacity, a set of ‘complex span’ measures were included in Experiment 5. Complex span tasks, most famously the ‘operation span’ (or ‘OSPAN’), measure the capacity of working memory for a given class of stimuli (e.g. letters) while attention is diverted to secondary demands. For example, in the OSPAN task participants remember a series of letters while also solving a series of mathematical sums. The tasks are designed in this way so as to specifically stress the capacity for executive control of working memory resources, as opposed to more traditional memory span measures which only tax the storage of information in memory. Executive working memory as measured by complex span tasks, is a well-established predictor of individual differences in a range of cognitively demanding tasks, including for example the Stroop task, spatial cuing, and task switching (e.g. Kane & Engle, 2001; Kane, Bleckley, Conway & Engle, 2001; Redick & Engle, 2006). The OSPAN task was also the measure used as a predictor of inattentional blindness in the studies described above.

Participants in Experiment 5 therefore completed a set of six tasks, three of which were designed to measure primarily perceptual capacity. These were an enumeration task, change blindness flicker task and an MOT task. The other three tasks were all designed to measure executive working memory capacity and were variations of the complex span tasks developed by Engle and colleagues (Turner & Engle, 1989; Unsworth et al. 2005), including operation span (OSPAN), reading span (RSPAN) and symmetry span (SSPAN) tasks. The combination of these tasks provides the opportunity for a measure of working memory which is not specific to a particular modality (numerical, lexical or spatial). Using three shortened WM tasks in place of a single full length task provides a more sensitive measure of the underlying capacity of interest (Oswald et al. 2015 and Foster et al. 2015).

4.2 Method

Participants

72 (43 female) participants aged 18 to 52 (mean = 24.42, SD = 6.99) were recruited from the UCL psychology research volunteer database. All participants provided written informed consent prior to taking part and were reimbursed £7.50 per hour for their time.

Procedure

The experiment was conducted in a quiet, dimly lit testing room where the participant was seated 60cm from the computer screen. Experimental tasks were run on a Dell PC with a 15-

inch flat screen monitor. Participants completed a total of six tasks: three complex span working memory tasks, an enumeration task, an MOT task and a change blindness task. The enumeration, MOT and change blindness tasks were all prepared in house using Matlab (Mathworks, Inc., Natick, MA) with the Cogent toolbox (www.vislab.ucl.ac.uk/cogent.php). The complex working memory span tasks were the same as those described by Oswald et al. (2015), downloaded from http://englelab.gatech.edu/tasks.html and presented using E Prime 2.0.

Enumeration task

Participants completed a visual enumeration task in which they were presented with a stimulus set of one to nine black squares of random sizes and positions around the centre of the screen. On each trial the squares were preceded by a fixation cross for 1 second, the enumeration set was then displayed for 200ms followed immediately by a black and white mask for 400ms and then a response screen for a further 2,400ms. Participants were instructed to respond by pressing a key on the keyboard number pad from 1-9 to indicate the number of squares; they were encouraged to be as accurate as possible while responding within the 3 second time limit. Thus the stimuli and trial procedure were identical to those of the enumeration task used in Chapter 3. Participants completed four experimental blocks of 81 trials (324 trials total); each block included an equal number of trials with each set size, in random order.

Change blindness task

In the change blindness task, participants were presented with alternating images of real world scenes which were presented for 200ms each with a grey rectangle presented for 100ms in between image presentations. In every second presentation of each image there could either be a small but conspicuous change or the image could be identical. The images alternated in this fashion for up to eight seconds or until the participant responded. Participants were instructed to respond by pressing the right or left shift keys of the keyboard respectively to indicate a whether or not there was a change. They were encouraged to be as accurate as possible but to respond as soon as they were confident of their answer. If no response was made the participant was required to guess ‘yes’ or ‘no’ at the end of the trial. After a response was made a green tick or red cross were presented in the centre of the screen for a correct or incorrect response respectively. The task was therefore identical to the one used in Chapter 3 except that the flickering presentation time was reduced to 8 seconds and participants were given the option of guessing ‘yes’ or ‘no’ if they ran out of time. An additional six trials were added making a total of 52 trials.

Multiple Object Tracking (MOT) task

In the MOT task a set of eight black dots were presented in random locations within a predefined movement area subtending 5.72 by 5.72 degrees in the centre of the screen. Each of the dots subtended 0.5 by 0.5 degrees and moved randomly at a rate of 2.15 degrees per second. They were deflected from the invisible boundaries of the movement area and from one-another such that no two dots ever overlapped.

Each trial of the MOT task (e.g. Figure 4.1) began with a central fixation cross presented for 1 second. The dots were then presented all in black, after 500ms four dots turned blue for 1,500ms, after which they turned back to black. After a further 500ms all of the dots began moving, the dots then ceased movement after 8 seconds and a single dot turned blue once again. Participants were instructed to press the ‘1’ key on the number pad if the probe was a target and the ‘2’ key if not, there was no response time limit and participants were encouraged to be as accurate as possible. Finally the probe turned either green or red to indicate whether the response was correct or incorrect respectively.

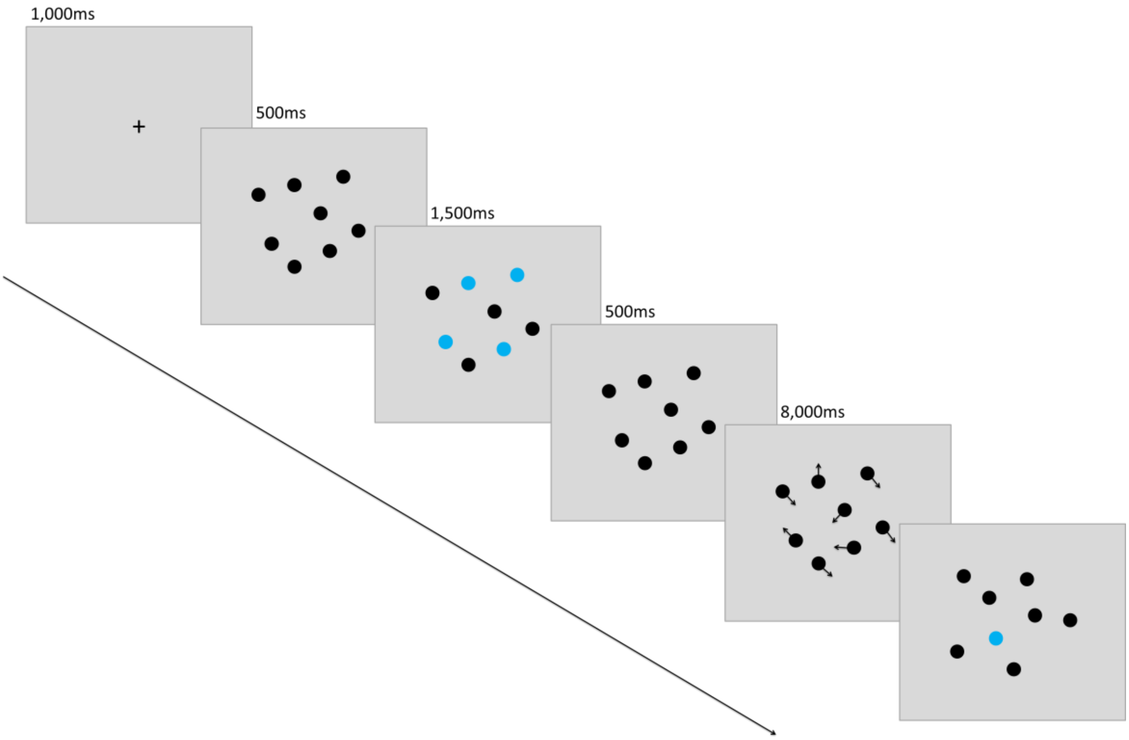

Figure 4.1 Schematic of the MOT task used in Experiment 5, eight dots are presented and four are cued as targets. Participants then track the dots as they move for eight seconds and respond to a subsequent probe.

Complex working memory span tasks

OSPAN

In the OSPAN task, participants were presented with a series of sums (e.g. (8/2)+9 = 13) in the centre of the screen along with boxes containing the words ‘True’ and ‘False’ (Figure 4.2). Each sum was followed by a single letter in the centre of the screen. After a variable number of sum and letter presentations (4-6) a memory response screen was presented which included 9 letters in random order. Participants were instructed to respond by clicking ‘yes’ or ‘no’ icons on-screen to indicate if the given answer was correct while also memorizing each of the letters in sequence. When the response screen was presented, participants were instructed to select the memorized letters in the order of their presentation. If the participant was uncertain of a given letter they were told to respond with ‘blank’.

RSPAN

The stimuli and trial procedure of the RSPAN task were identical to those of the OSPAN task however instead of sums the participant was presented with sentences (which were in turn followed by a letter). Participants were instructed to indicate whether or not the sentence made semantic sense (e.g. “The prosecutor’s dish was lost because it was not based on fact.” – Oswald et al. 2015), and memorize each letter in sequence. The memory response screen was identical to that of the OSPAN task (Figure 4.2).

SSPAN

In the SSPAN task participants were presented with a series of black and white block images made up of an eight by eight grid of black and white squares. Each of these images was followed by another image made up of a four by four grid of white (and one red) squares. Finally, after a variable number of (3-5) of trials, the participant was presented with a response screen including a four by four grid of white squares.

Participants were instructed to report whether the left and right sides of the black and white images were symmetrical by clicking the ‘yes’ or ‘no’ icons as in the OSPAN and RSPAN tasks. They were then instructed to memorize the position of the red square in the following grid image, they then selected these positions by clicking them on the response screen.

In each complex working memory span task, the experimental trials were preceded by a series of practice sessions. First, participants practiced the ‘operation’ component (sums, reading or symmetry judgement) alone with no memory stimuli, then the ‘memory’ component with no operations and finally both together as in experimental trials. The average reaction time from the final practice section plus two standard deviations was used as the time limit in experimental trials. There were a total of 30 experimental trials in the OSPAN and RSPAN tasks and 24 trials in the SSPAN task. The participant's accuracy (% correct) in the operation (sum, reading or symmetry judgement) portion of the task was displayed throughout the task in the upper right corner and they were instructed to maintain a minimum score of 80% (this is recommended as a cut-off to ensure that participants are attending both aspects of the task as instructed).

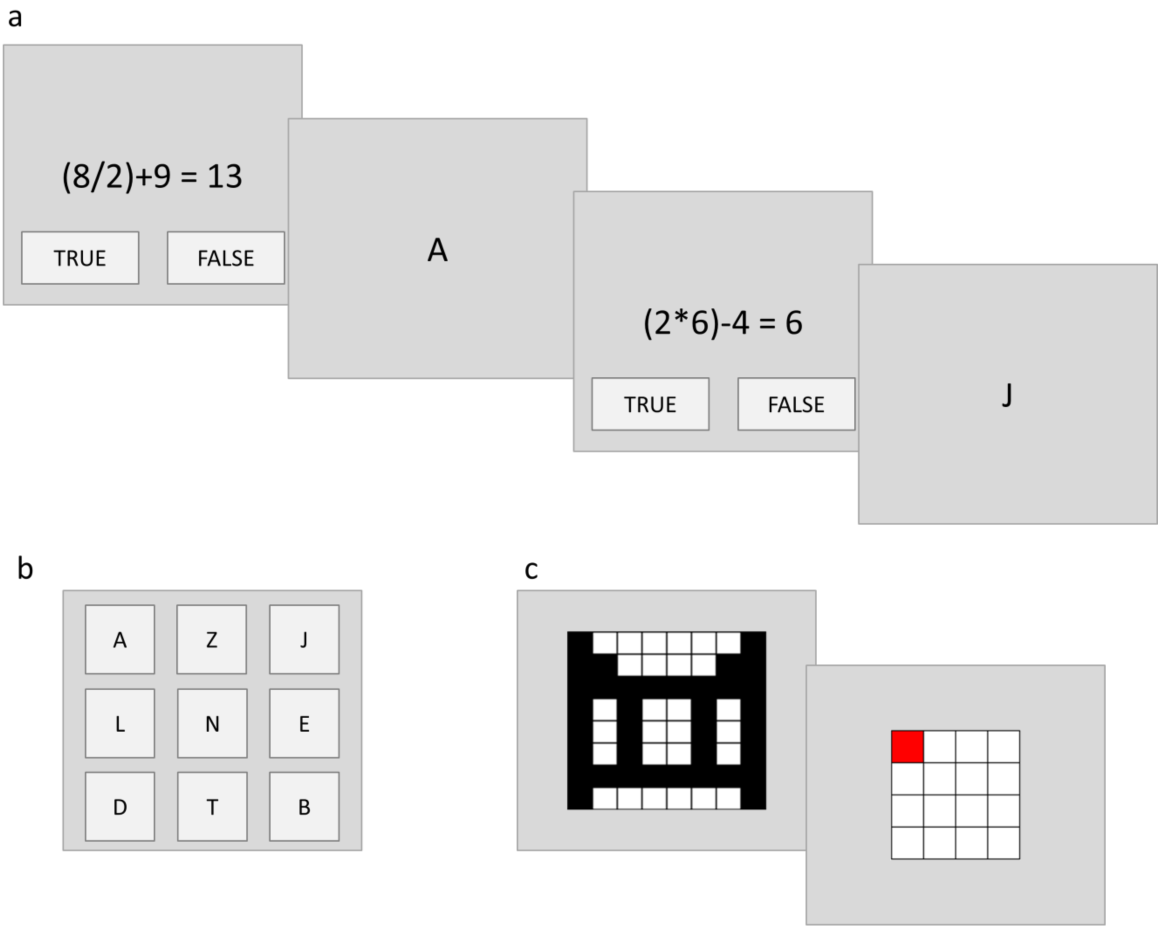

Figure 4.2 A schematic of a typical trial in the OSPAN task (a), participants perform a series of sums and memorise subsequently displayed letters. After a variable number of trials a memory test screen (b) is presented. In the SSPAN task symmetry judgements take the place of sums and location probes take the place of letter memoranda (c).

4.3 Results

4 participants (3 male) failed to meet the inclusion criterion of 60% correct responses in the lowest set size of the enumeration task. The sample analysed was therefore n = 68, aged 18-52 (mean = 24.62, SD = 7.12), of whom 42 were female.

Enumeration task performance

Average accuracy at each set size in the enumeration task is presented in Table 4.1, a bilinear function fit to each participant's accuracy data for set sizes 1-8 yielded an average RMSE of 8.26 (SD = 4.75) and an average adjusted R^2 value of .76 (SD = .22), indicating a good fit of the model to the data. The average subitizing capacity estimated by the bilinear fit was 3.17 (SD = 0.84) and average estimation accuracy was 49.10 (SD = 14.35), both within the range of estimates from previous experiments.

Set size	**Average accuracy (SD)**
1	93.11% (8.80)
2	94.93% (7.18)
3	89.85% (14.43)
4	69.56% (23.04)
5	54.28% (20.19)
6	46.00% (20.14)
7	32.63% (18.82)
8	26.79% (16.41)
9	30.58% (25.63)

Table 4.1 Average performance for each set size in the enumeration task of Experiment 5.

Change blindness task performance

Change blindness task performance is presented in Table 4.2, detection sensitivity was calculated using a non-parametric measure (A) along with the corresponding measure of bias (b) as in Chapter 3.

Measure	**Mean (SD)**
Detection rate	50% (12)
False alarm rate	1% (9)
Sensitivity (A)	.82 (.08)
Bias (b)	2.41 (0.69)

Table 4.2 Average performance metrics in the change blindness task of Experiment 5.

MOT task performance

Average accuracy in the MOT task was 75.19% (SD = 12.76). Tracking capacity was estimated using the 'Effective Number of Objects Tracked' (ENOT) calculated from the formula described by Scholl, Pylyshyn and Feldman (2001). ENOT scores were calculated as: $m = n(2p-1)$, where m is the estimated tracking capacity (ENOT), n is the number of target dots and p is the proportion of correct responses. The average ENOT capacity score was 1.90 (SD = 0.84).

Complex span task performance

Performance metrics for each of the complex span tasks is presented in Table 4.3. The ‘total’ score was used as this has been established as the best measure of capacity by previous research (Redick et al. 2012). For each of the tasks the total score is the total number of memory stimuli (letters or square positions) reported in the correct sequential position (ignoring incorrect or ‘Blank’ items). SSPAN score is necessarily lower as the task includes fewer overall trials. The maximum possible scores are 30 for the OSPAN and RSPAN tasks and 24 for the SSPAN task. Average accuracy on the ‘operation’ portion of the tasks was above 95% for all of the tasks, no participant scored below 80% as instructed.

Task	Score (SD)	Accuracy % (SD)
OSPAN	25.27 (5.34)	96.74 (3.48)
RSPAN	23.50 (4.51)	95.81 (3.90)
SSPAN	18.09 (4.62)	98.04 (2.65)

Table 4.3 Average memory span scores and operation accuracy in each of the complex span tasks of Experiment 5.

4.3.1 Predicting change blindness from subitizing capacity

Detection rate

The first analysis sought to test whether subitizing is a significant predictor of change detection rate when controlling for executive working memory capacity. A multiple regression was conducted which included only the working memory span scores as control variables in its first step, subitizing capacity and estimation accuracy were then added in a second step. The full regression is presented in Table 4.4, the first step did not significantly predict change blindness ($R^2 = .02$, $p > .05$), indicating that there was no relationship between working memory span scores and change detection rate. The second step did significantly predict detection rate (R^2change = .24, $p < .001$). As can be seen in Table 4.4 subitizing and estimation accuracy were the only significant unique predictors. This replicates the results of Chapter 2 (Experiment 3) while also controlling specifically for executive working memory capacity, confirming the distinct relationship between subitizing and change blindness.

Model	**Variable**	**Beta**	**T**	**Sig.**
1	Constant		4.585	<.001
$R^2 = .02$, $p > .05$	OSPAN	-.032	-.224	.823
	RSPAN	.059	.424	.673
	SSPAN	.108	.806	.423
2	Constant		2.641	.010
R^2change = .24, $p < .001$	OSPAN	.028	.206	.837
	RSPAN	-.126	-.950	.346
	SSPAN	-.006	-.048	.962
	Estimation	.310	2.469	.016
	Subitizing	.390	3.270	.002

Table 4.4 Results of a multiple regression predicting change blindness from complex span working memory capacity, subitizing and estimation accuracy in Experiment 5.

Detection sensitivity

The same analysis was repeated but this time predicting change blindness detection sensitivity. The results are presented in Table 4.5, once again the first step did not significantly predict detection sensitivity (step 1: $R^2 = .01$, $p > .05$), indicating no relationship between working memory and change blindness. The second step did significantly predict detection sensitivity (R^2change = .10, p < .05). As can be seen in Table 4.5 subitizing was the only significant unique predictor, indicating that this was the only variable for which the relationship with change detection cannot be explained by general factors or working memory. Broadly these results replicate those of the analysis using detection rate, with the exception that estimation accuracy is no longer a significant unique predictor of change blindness. There was no relationship between response bias (b) in the change blindness task and either subitizing (r(68) = -.05, p > .05) or estimation accuracy (r(68) = -.14, p > .05).

Model	**Variable**	**Beta**	**T**	**Sig.**
1	Constant		12.692	<.001
R^2 = .005, p > .05	OSPAN	.035	.242	.810
	RSPAN	.014	.099	.921
	SSPAN	.046	.340	.735
2	Constant		10.334	<.001
R^2change = .104, p < .05	OSPAN	.091	.625	.534
	RSPAN	-.117	-.811	.420
	SSPAN	-.019	-.138	.891
	Estimation	.165	1.210	.231
	Subitizing	.293	2.264	.027

Table 4.5 Results of a multiple regression predicting change blindness detection sensitivity from complex working memory span scores, estimation accuracy and subitizing capacity.

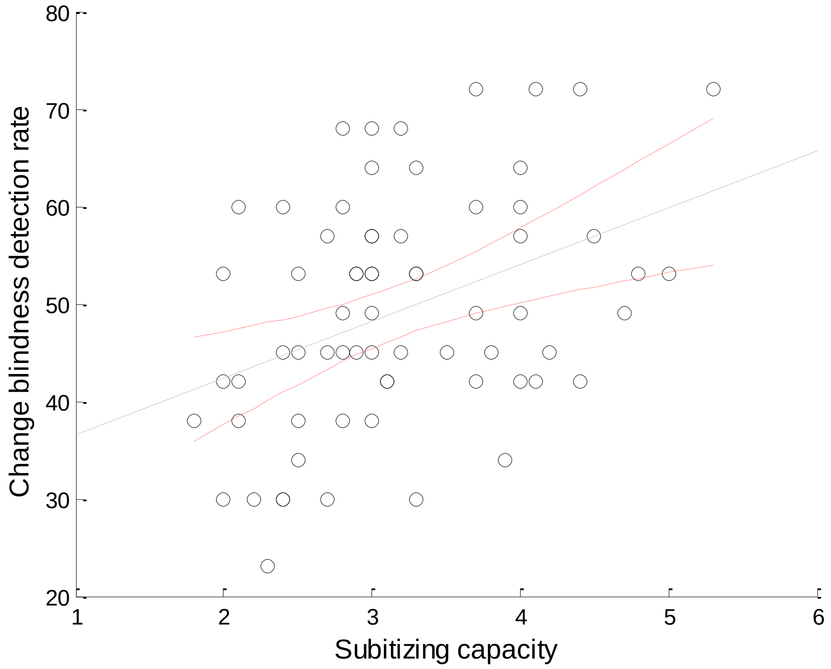

Figure 4.3 Scatterplot of the correlation between change detection rate and subitizing capacity in Experiment 5 (red dashed lines indicate 95% confidence intervals).

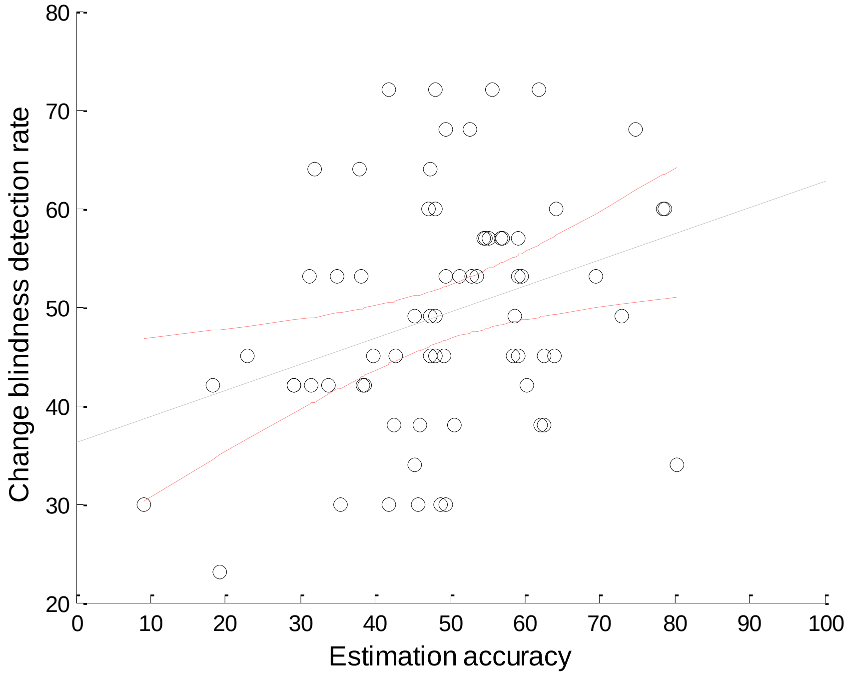

Figure 4.4 Scatterplot of the correlation between change detection rate and estimation accuracy in Experiment 5 (red dashed lines indicate 95% confidence intervals).

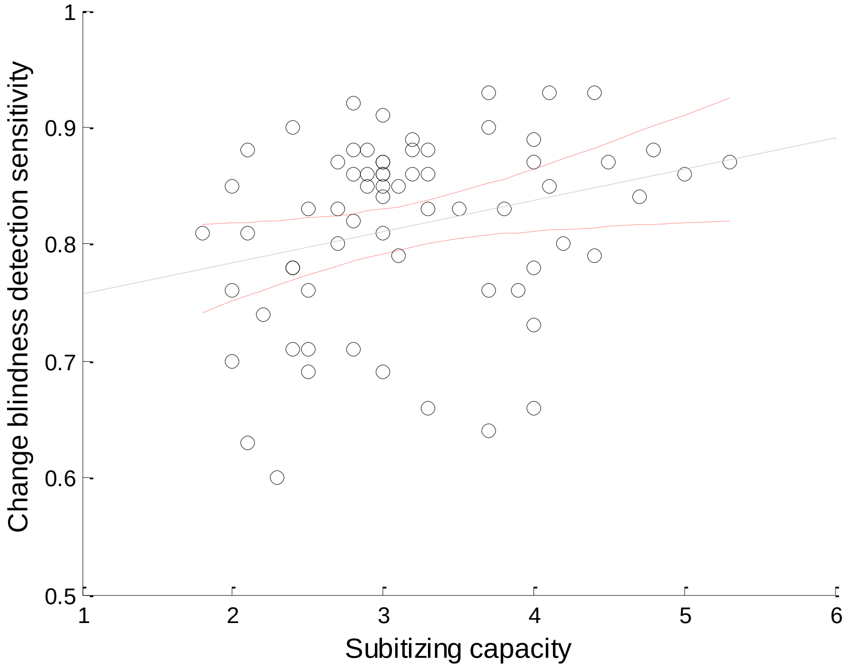

Figure 4.5 Scatterplot of the correlation between change detection sensitivity and subitizing capacity in Experiment 5 (red dashed lines indicate 95% confidence intervals).

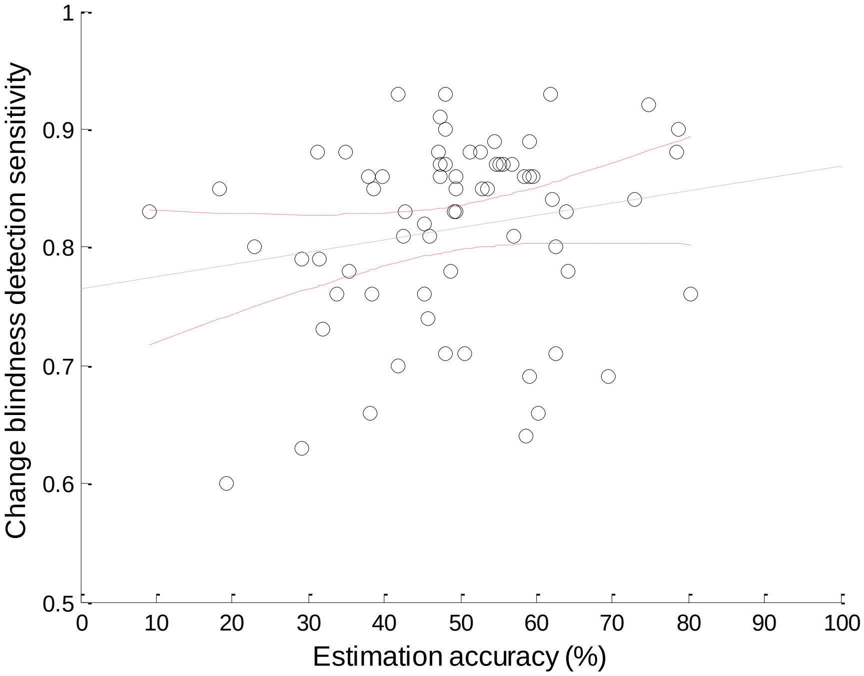

Figure 4.6 Scatterplot of the correlation between change detection sensitivity and estimation accuracy in Experiment 5 (red dashed lines indicate 95% confidence intervals).

4.3.2 Predicting MOT from subitizing capacity

The next analysis was intended to establish whether or not perceptual capacity as measured by subitizing is common to non-transient, continuous displays in the MOT task. Once again a multiple regression was used which included working memory span scores in its first step as control variables; the second step included subitizing and estimation accuracy as in previous analyses. The full regression is presented in Table 4.6, the first step was significant ($R^2 = .13$, $p < .05$), indicating a significant relationship between span scores and MOT performance. More importantly the second step was also significant (R^2change = .14, $p < .005$) and subitizing was the only predictor which accounted for significant unique variance. Thus, common variance between subitizing and MOT capacity is separate from any variance associated with working memory capacity. Working memory capacity was significantly associated with MOT performance; a relationship most likely attributable to non-domain specific working memory capacity as no one individual measure (OSPAN, RSPAN or SSPAN score) accounted for significant unique variance.

Model	**Variable**	**Beta**	**t**	**Sig.**
1	Constant		.085	.933
$R^2 = .13$, $p < .05$	OSPAN	.134	.996	.323
	RSPAN	.187	1.429	.158
	SSPAN	.156	1.240	.219

2	Constant		-1.559	.124
R^2change = .14, p < .005	OSPAN	.210	1.599	.115
	RSPAN	.032	.247	.806
	SSPAN	.090	.732	.467
	Estimation	.160	1.303	.198
	Subitizing	.361	3.088	.003

Table 4.6 Results of a multiple regression predicting MOT performance from subitizing capacity

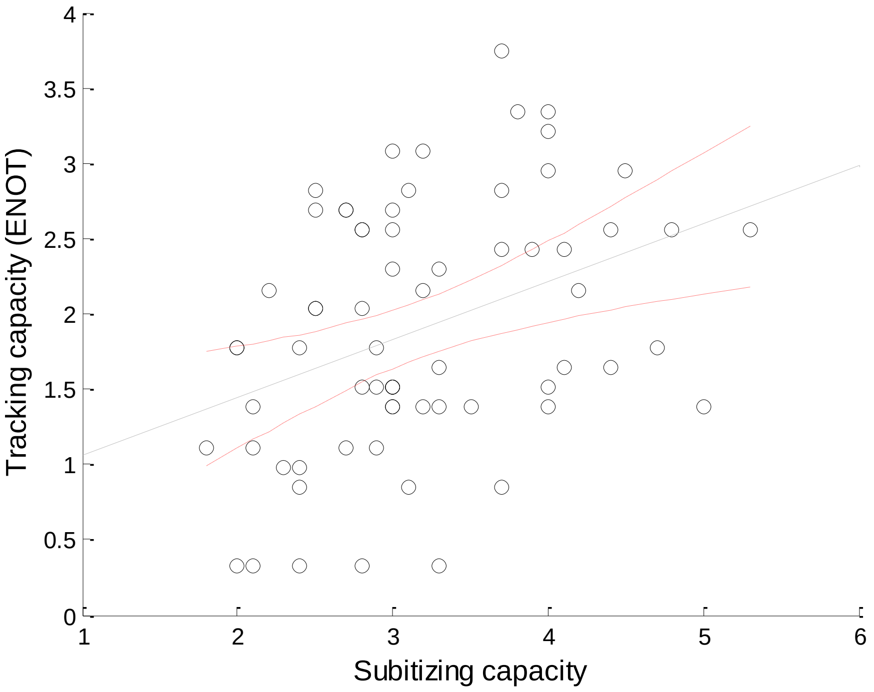

Figure 4.7 Scatterplot of the correlation between subitizing capacity and number of objects tracked (ENOT) in Experiment 5 (red dashed lines indicate 95% confidence intervals).

4.3.3 Testing the general perceptual capacity hypothesis

Detection rate

The load theory hypothesis predicts that individual differences in MOT, change detection and subitizing performance should all share variance which should be distinct from any variance accounted for by working memory span (or estimation accuracy). To confirm this it is necessary to establish the relationship between MOT and change blindness and to establish that this relationship is not be attributable to working memory capacity but rather to perceptual capacity as previously measured with subitizing. Therefore MOT capacity should predict change detection performance when controlling for working memory span, but not when controlling for subitizing capacity.

The first part of this hypothesis was tested with a regression which predicted change detection rate with working memory span scores and estimation accuracy in its first step (thus controlling for executive working memory capacity and general cognitive factors but not perceptual capacity) and tracking capacity (ENOT) in the second step. Only the second step of the regression was significant (Table 4.7, R^2 change = .05, $p < .05$), indicating that MOT significantly predicted change detection rate when controlling for working memory capacity and estimation accuracy. In the final model, both MOT and estimation accuracy accounted for significant unique variance, indicating that both share variance with change detection rate which cannot be attributed to working memory. Importantly, this is the same profile as observed with subitizing, supporting the hypothesis of a shared perceptual capacity.

Model	**Variable**	**Beta**	**t**	**Sig.**
1	Constant		4.382	<.001
R^2= .06, p > .05	OSPAN	-.090	-.651	.518
	RSPAN	.015	.113	.910
	SSPAN	-.002	-.011	.991
	Estimation	.352	2.628	.011
2	Constant		4.518	<.001
R^2change = .05, p < .05	OSPAN	-.116	-.852	.398
	RSPAN	-.026	-.196	.845
	SSPAN	-.025	-.193	.848
	Estimation	.301	2.262	.027
	MOT	.254	2.007	.049

Table 4.7 Results of a multiple regression predicting change blindness detection rate from MOT capacity controlling for complex working memory span and estimation accuracy

A further regression (Table 4.8) tested the second prediction: that subitizing accounts for the common variance between MOT and change blindness. This regression included working memory span scores, estimation accuracy and subitizing as control variables in its first step and MOT in a second step. Neither the first or second steps were significant (R^2change < .11, p’s > .05) indicating that MOT no longer contributes unique variance to the prediction of change blindness when controlling for subitizing. Only subitizing capacity and estimation accuracy accounted for significant unique variance in the final model, replicating previous analyses (Experiment 3 and the first analysis of the present chapter).

Model	**Variable**	**Beta**	**t**	**Sig.**
1	Constant		2.641	.010
$R^2 = .18, p< .005$	OSPAN	.028	.206	.837
	RSPAN	-.126	-.950	.346
	SSPAN	-.006	-.048	.962
	Estimation	.310	2.469	.016
	Subitizing	.390	3.270	.002
2	Constant		2.779	.007
R^2change = .01, $p > .05$	OSPAN	.001	.007	.994
	RSPAN	-.130	-.980	.331
	SSPAN	-.017	-.138	.890
	Estimation	.289	2.275	.026
	Subitizing	.344	2.686	.009
	MOT	.127	.979	.332

Table 4.8 Results of a multiple regression predicting change blindness detection rate from MOT capacity controlling for working memory capacity, estimation accuracy and subitizing capacity.

Detection sensitivity

The same analyses were repeated, this time predicting change blindness detection sensitivity in place of detection rate. Again the first regression included working memory span scores and estimation accuracy in its first step and tracking capacity (ENOT) in the second step. Only the second step of the regression was significant (Table 4.9), indicating that MOT significantly predicted change detection sensitivity (R^2change = .07, $p < .05$) when controlling for working memory capacity. Only MOT was a significant unique predictor in this analysis as there was no significant relationship between estimation accuracy and change detection sensitivity (as was established in the first set of analyses in this chapter).

Model	**Variable**	**Beta**	**t**	**Sig.**
1	Constant		12.471	<.001
R^2= .04, $p > .05$	OSPAN	.002	.016	.987
	RSPAN	-.011	-.076	.940
	SSPAN	-.015	-.110	.913
	Estimation	.197	1.407	.164
2	Constant		12.887	<.001
R^2change = .07, $p < .05$	OSPAN	-.027	-.192	.848
	RSPAN	-.058	-.420	.676
	SSPAN	-.043	-.312	.756
	Estimation	.139	1.004	.319
	MOT	.291	2.218	.030

Table 4.9 Results of a multiple regression predicting change detection sensitivity from MOT controlling for estimation accuracy and complex span scores.

The second regression (Table 4.10) once again tested the prediction that subitizing accounts for the common variance between MOT and change blindness. As previously, the second step was not significant (R^2change = .03, p’s > .05) indicating that MOT did not account for significant unique variance in change detection sensitivity when controlling for subitizing. Only subitizing capacity accounted for significant unique variance in the final model.

Model	**Variable**	**Beta**	**t**	**Sig.**
1	Constant		10.334	<.001
$R^2 = .11, p < .05$	OSPAN	.091	.625	.534
	RSPAN	-.117	-.811	.420
	SSPAN	-.019	-.138	.891
	Estimation	.165	1.210	.231
	Subitizing	.293	2.264	.027
2	Constant		10.536	<.001
R^2change = .03, $p > .05$	OSPAN	.047	.317	.752
	RSPAN	-.123	-.867	.390
	SSPAN	-.038	-.279	.781
	Estimation	.131	.959	.341
	Subitizing	.217	1.577	.120
	MOT	.211	1.513	.135

Table 4.10 Results of a multiple regression predicting change blindness detection sensitivity from MOT while controlling for estimation accuracy, subitizing capacity and complex span scores.

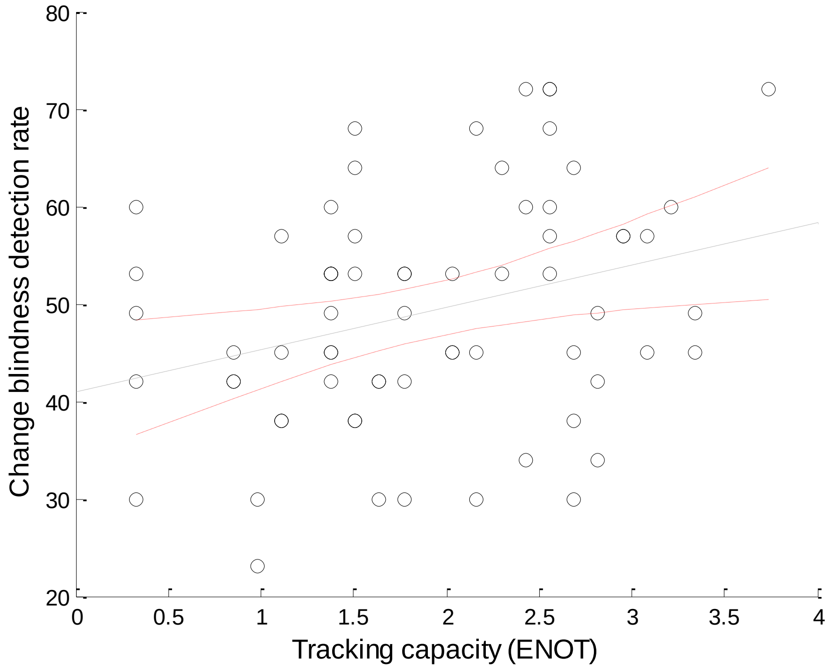

Figure 4.8 Scatterplot of the correlation between MOT and change blindness detection rate in Experiment 5 (red dashed lines indicate 95% confidence intervals).

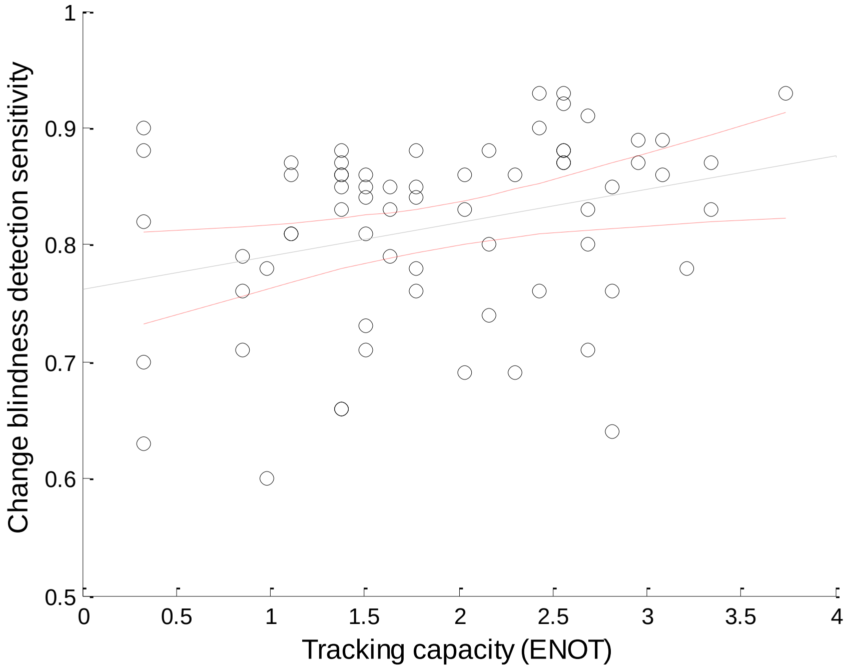

Figure 4.9 Scatterplot of the correlation between change blindness detection sensitivity and MOT performance in Experiment 5 (red dashed lines indicate 95% confidence intervals).

4.4 Conclusions

The results of Chapter 4 support the conclusion that a common resource underlies performance of perceptually loading tasks and that this resource is distinct from working memory or general cognitive factors. MOT and subitizing both had similar profiles as predictors of change blindness and all three perceptual tasks shared unique variance which could not be accounted for by working memory capacity.

Executive working memory was not a significant predictor of change detection, supporting the conclusion that the primary determinant of subjective awareness is a distinct perceptual resource. This is in replication of previous investigations such as that by Pringle et al. (2001) which found no relationship between executive control and change blindness when controlling for lower-level processing (e.g. attention or VSTM). This also supports the suggestion that the role of executive working memory in inattentional blindness demonstrated previously by Hannon et al. (2010) and Seegmiller et al. (2011) may be due to the working memory load inherent in their task. These results replicate those of Chapter 3 (Experiment 3) in establishing subitizing as a unique predictor of change detection when controlling for variance associated with more general factors (by controlling for working memory capacity and estimation performance).

Subitizing also shared significant unique variance with MOT performance after controlling for any contribution of working memory to the tasks. Interestingly, although no individual complex span task was a significant unique predictor of MOT performance, there was still a significant relationship between MOT and working memory span in general. This may suggest that successful performance of the MOT task relies on both perceptual and working memory capacity, perhaps in coordinating the deployment of perceptual resources over time.

This lends further support to the conclusion that working memory load is inherent in the sustained inattentional blindness task, which involves similar object tracking. Nevertheless, the unique relationship between subitizing and MOT supports the conclusion of a common underlying perceptual resource.

Finally, MOT was established as a parallel measure of perceptual capacity, predicting change blindness with a similar profile to subitizing. Like subitizing, MOT was a significant predictor of change detection when controlling for executive control. However, the unique variance shared by change blindness and MOT was eliminated when controlling for subitizing capacity. Thus it appears that perceptual capacity as measured by subitizing mediates the relationship between MOT and change blindness. This result provides further evidence that a common capacity limit underlies perceptually loading tasks (MOT, subitizing, change blindness) which is distinct from variance related to higher cognitive processes (complex span) or other general performance factors.

Chapter 5

Brain structural correlates of capacity

5.1 Chapter introduction

The behavioural results thus far have been consistent with a perceptual capacity common to a variety of behavioural measures but distinct from other cognitive resources such as executive working memory. In addition to the common variance in behavioural performance observed here, many of these tasks have been associated with brain activity in specific cortical areas in previous research. In Chapter 5 I therefore sought to establish the brain-structural correlates of individual differences in perceptual and executive capacities as measured using the tasks established in previous chapters. A new sample of participants completed the same change blindness, enumeration, MOT and complex span tasks as described in Chapter 4 before also undergoing structural MRI brain scans. Individual differences in behavioural performance were analysed using exploratory factor analysis to further establish the shared variance in performance. These measures were then used as predictors of regional grey and white matter density throughout the brain using Voxel-Based Morphometry (VBM) analyses.

Previous research has established effects of load on processing in early sensory cortices (e.g. Schwartz et al. 2005; Kelley & Lavie, 2010). These investigations measured retinotopic activity in primary visual cortex to establish that increased perceptual load leads to significantly reduced distractor-related activity (Rees et al. 1997; Schwartz et al. 2005) and working memory load leads to increased activity (Kelley & Lavie, 2010). Thus the effects of perceptual and cognitive load on early sensory brain activity mirror the behavioural effects. However, many of these studies also detect significant load-related activity changes in parietal cortex as well as some regions of frontal cortex. Change detection (relative to change blindness) for face and place images has been associated with activity in frontal and parietal regions as well as category specific visual cortices (Beck et al. 2001). The causal role of parietal involvement in change blindness was later confirmed using magnetic stimulation

(Beck, Muggelton, Walsh & Lavie, 2005): stimulation of right (but not left) parietal cortex resulted in significantly increased rates of change blindness.

Neuroimaging studies of subitizing, MOT and related paradigms have repeatedly found that activity in parietal cortex, notably the right temporo-parietal junction (TPJ) is significantly modulated by load in these tasks. For example, influential studies by Jovicich et al. (2001) and Culham et al (2001) established a variety of parietal and frontal regions in which activity is linearly increased with increased tracking load in the MOT task. Similarly, Todd et al. (2005) established parametric modulations in right TPJ activity with increasing VSTM load, which was also associated with increased inattentional blindness for unexpected stimuli. Finally, a recent study by Vetter et al. (2011) established that right TPJ activity was selectively modulated by set size within the subitizing range (up to four items) but not for higher sets. Thus, activity in the TPJ appears to represent a limiting factor in attentional processing capacity, in line with load theory. Executive control has long been associated with the frontal cortex (Yuan & Raz, 2014) and tasks requiring top-down control of attention are routinely shown to elicit frontal cortical activity (e.g. De Fockert, Rees, Frith & Lavie, 2004; Chein, Moore & Conway, 2011).

By investigating individual differences in brain structure, it is possible to identify those brain areas associated with individual differences in capacity, as opposed to areas simply active during task performance. As discussed in the General Introduction, voxel-based morphometry (VBM) analysis provides a means of measuring the cortical density throughout the brain to identify areas associated with behavioural performance. The behavioural results from chapters 3 and 4 established common variance between tasks which was attributed to independent underlying constructs of perceptual and executive capacities. I therefore predicted that these behavioural individual differences would be associated with dissociable brain-structural correlates. Based on findings from previous literature, which used primarily functional imaging techniques, I predicted that perceptual capacity would be associated with regional differences within the parietal cortex, especially the TPJ of the right hemisphere, whereas correlates of executive control would be more focused in the frontal/ prefrontal cortex.

5.2 Method

Participants

A new sample of n = 44 people participated in Experiment 6; participants were aged 18 to 43 (mean = 25.73, SD = 5.86) and 24 were female. All participants provided written informed consent prior to both the behavioural testing session and the MRI scan and were reimbursed £7.50 per hour for their time.

Behavioural testing

Participants completed the same six tasks as described in Chapter 4 and under the same testing conditions. Behavioural testing was conducted in a quiet and dimly lit testing room; the six computer tasks were all run on a Dell PC with a 15-inch flat screen monitor and participants were seated 60cm from the screen. Behavioural testing preceded the MRI scan by approximately one week except for 4 participants who completed both parts of the experiment on the same day.

Image acquisition

Brain images were acquired at the Birkbeck/ UCL Centre for Neuroimaging (BUCNI) using a 1.5 Tesla (Siemens Avanto) MRI scanner, with a 32-channel head coil. The whole brain was imaged using a high resolution T1-weighted 3D magnetization-prepared rapid acquisition gradient-echo sequence (MPRAGE; voxel size = 1.00 x 1.00 x 1.00 mm).

Image pre-processing

The T1-weighted scans were first segmented into separate tissue types using SPM12's segmentation tool, which uses 6 tissue classes to optimally characterize the voxels of interest. This was followed by inter-subject registration of the grey and white matter images independently using Diffeomorphic Anatomical Registration Through Exponentiated Lie Algebra (DARTEL; Ashburner, 2007; Ashburner & Friston, 2000) also in SPM12. During co-registration the local grey and white matter volumes are conserved by modulating the intensity at each voxel by the Jacobian determinants of the deformation fields as computed by DARTEL. The co-registered images were smoothed using a Gaussian kernel (FWHM = 10mm) before being transformed to MNI stereotactic space in SPM12 through affine nonlinear spatial normalisation.

5.3 Behavioural Results

Enumeration performance

Average accuracy at each set size of the enumeration task is presented in Table 5.1 and Figure 5.1. The bilinear function fit to the accuracy data for each participant produced an average RMSE of 9.01% (SD = 5.13) and an average adjusted R^2 value of 0.88 (SD = 0.11). The average subitizing capacity was 3.06 (SD = 0.65, range: 1.7 - 4.5). Average accuracy in estimation of set sizes beyond the participant's subitizing capacity was 54.20% (SD = 10.76).

Set size	**Average accuracy (% correct) (SD)**
1	93.94 (7.70)
2	94.60 (6.88)
3	89.87 (13.40)
4	70.08 (19.15)
5	54.26 (15.76)
6	51.33 (15.19)
7	39.39 (13.34)
8	34.56 (16.19)
9	40.53 (21.89)

Table 5.1 Average accuracy and corresponding standard deviation for each set size of the enumeration task.

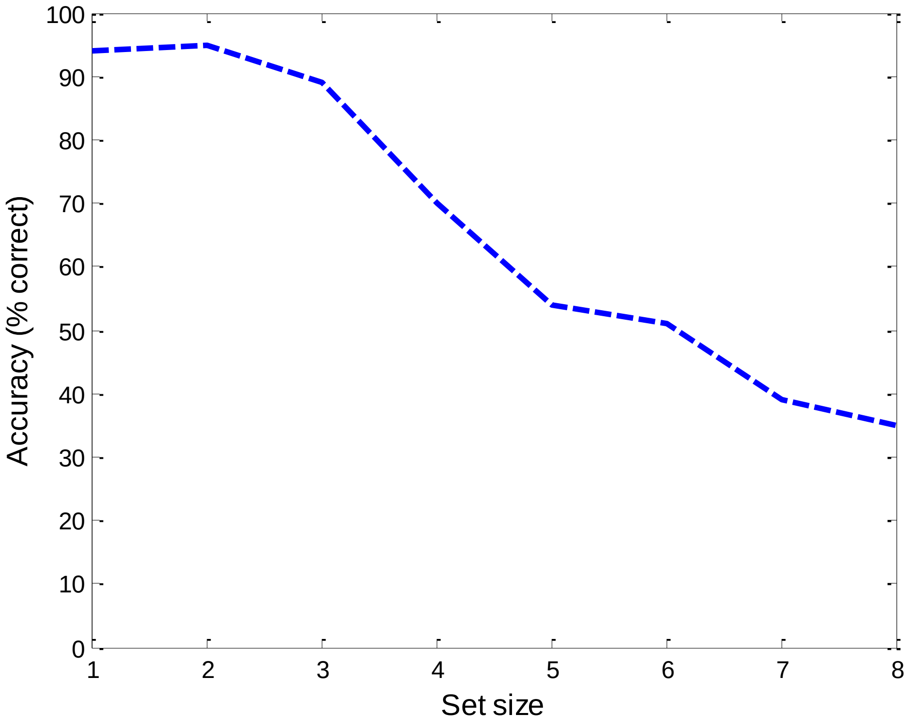

Figure 5.1 Accuracy as a function of set size in the enumeration task of Experiment 6.

Change blindness performance

Change detection performance was measured using a non-parametric measure of detection sensitivity (A; Zhang & Mueller, 2005) as in previous chapters. The average detection sensitivity for the sample was .83 (SD = .07; range: .69 - .94).

MOT performance

Average accuracy in the MOT task was 75.69% (SD = 9.44), average tracking capacity calculated using the ENOT formula (as in Chapter 4) was 2.06 (SD = 0.76; range: 0.3 - 3.18).

Complex span performance

Average performance data for the OSPAN, RSPAN and SSPAN tasks are presented in Table 5.2 expressed as total scores for which the maximum is 30 for OSPAN and RSPAN and 24 for the SSPAN task. Accuracy in the 'operation' portion of each task (i.e. sums, reading and symmetry judgements) is also presented. Operation accuracy was consistently above 90% and did not drop below 80% for any participant, indicating that they attended both components of the task as instructed.

Task	**Score (SD)**	**Accuracy (SD)**
OSPAN	25.65 (4.45)	92.27% (5.32)
RSPAN	24.88 (4.47)	92.88% (6.92)
SSPAN	17.25 (4.40)	93.08% (5.75)

Table 5.2 Average scores and accuracy in the complex working memory span tasks.

5.3.1 Principal components analysis of behavioural measures

The results of Chapter 4 suggested two underlying constructs, one representing perceptual capacity and another representing the capacity for cognitive control. This result could be better understood using factor analysis techniques to establish the latent structure in the relationships between behavioural variables. Factor analysis techniques require large sample sizes to be reliable (Field, 2009; Tabachnick & Fidell, 2001), and so this analysis was not possible with the sample in Chapter 4. The behavioural tasks and testing procedure were identical in chapters 4 and 5; and independent samples t-tests indicated that there was no significant difference in performance of any of the key measures of interest (all t's < 1.60, all p's > .05). By combining the two samples it was therefore possible to obtain a sufficient sample size to analyse the latent structure of the relationships observed in Chapter 4. Behavioural performance scores were thus entered into a principal components analysis with orthogonal (Varimax) factor rotation. The Keyser-Meyer-Olkin measure of sampling adequacy indicated that the sample size was adequate (KMO = .66; Keiser, 1970; Field, 2009). Bartlett's test for sphericity was significant, ($\chi^2(15) = 91.10$, $p < .001$), indicating that inter-item correlations were sufficient for PCA.

Principal components were extracted with Eigenvalues greater than one (Keiser, 1964), resulting in a two factor solution; which was supported by examination of a scree-plot (Figure 5.2) in which there is a clear point of inflexion at the third factor. The first factor accounted for 36.09% of the overall variance and the second factor accounted for 21.01% (57.10% cumulatively).

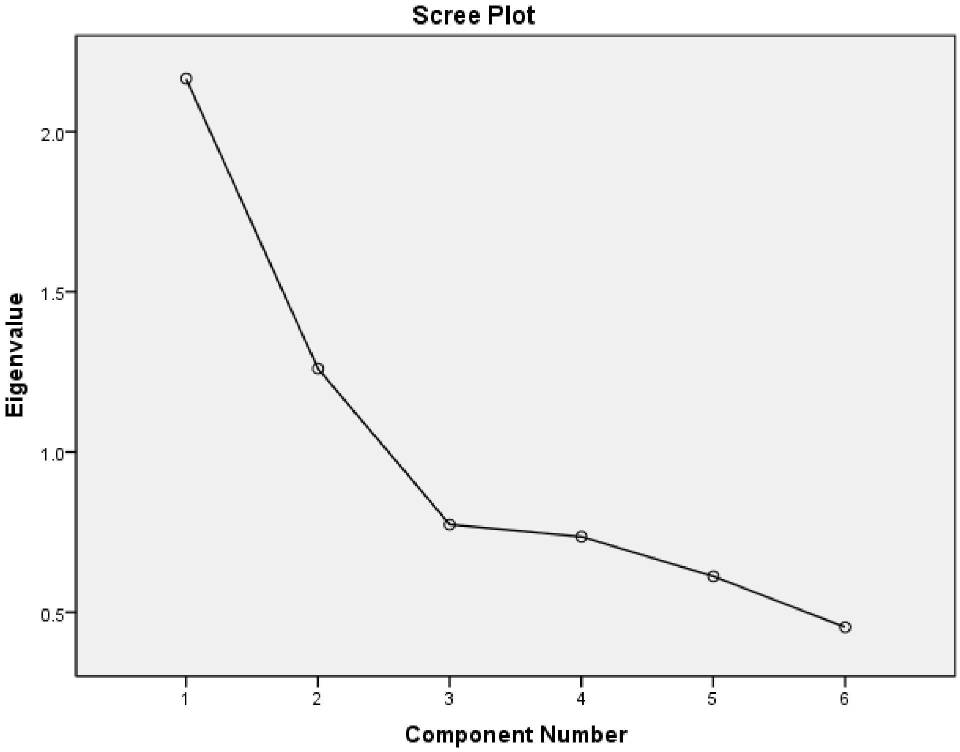

Figure 5.2 A scree plot displaying Eigenvalues for each possible component in the factor analysis of behavioural data. Two factors had Eigenvalues greater than 1, and there is a clear distinction between these two and subsequent factors (scree) in the plot, consistent with a two factor solution.

Rotated factor loadings are displayed in Table 5.3 and Figure 5.3. Factor loadings greater than .51 are considered significant with a sample greater than n = 100 (Stevens, 2002), by this criterion the first component consists solely of the three complex span scores, which also have very low and non-significant loadings on the second factor. The second factor consists of subitizing, change blindness and MOT scores each of which has loadings higher than .60. MOT score has a slight loading on factor one (which still does not meet the criteria of .51 to be considered significant) but a much stronger loading on factor two.

These results indicate two separate cognitive constructs which represent executive working memory (Factor 1) and perceptual (Factor 2) capacities, which is in good accordance with the original hypothesis. The slight (but non-significant) cross loading of MOT may indicate that both of these capacities are separately important for performance of this task, which is consistent with the fact that working memory span was a significant predictor of tracking capacity in the second analysis of Chapter 4.

Measure	**Factor 1 loading**	**Factor 2 loading**
OSPAN	.84*	-.07
RSPAN	.73*	.18
SSPAN	.65*	.16
Subitizing	.01	.78*
Change blindness	.03	.72*
MOT	.36	.68*

Table 5.3 Rotated factor loadings for the exploratory factor analysis of behavioural data combined across samples from chapters four and five. An asterisk signifies a significant loading by the criteria of Stevens (2002); the only trend toward cross-loading is of MOT on Factor 1.

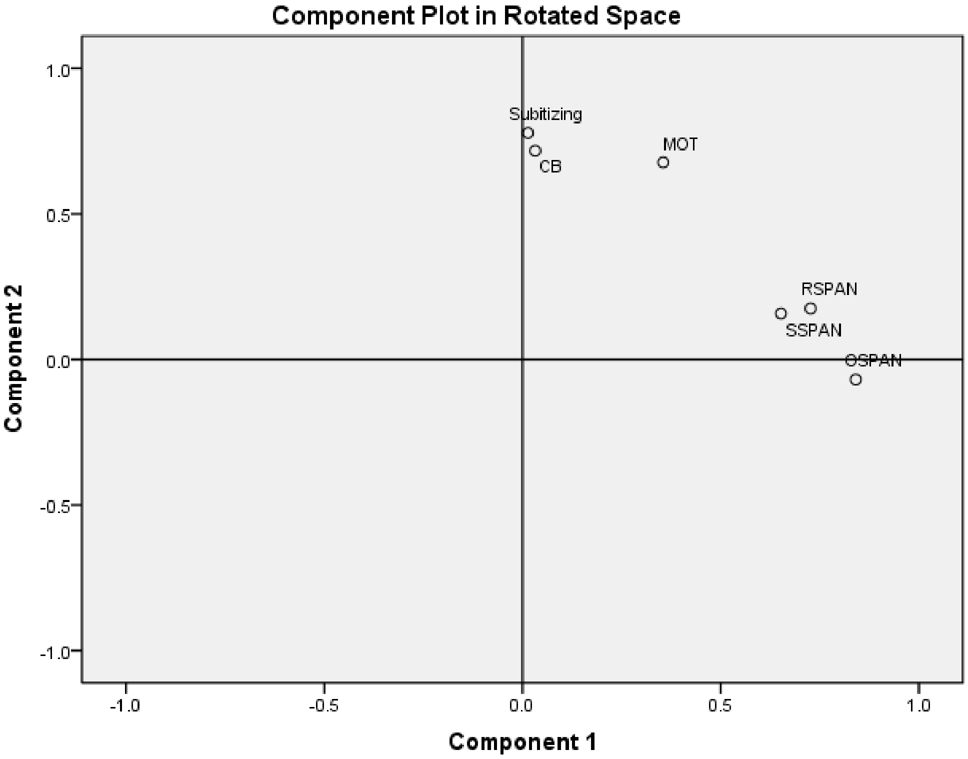

Figure 5.3 A component loading plot displaying factor loadings of each variable in Varimax rotated component space. Subitizing and change blindness (CB) load strongly on component one, span scores load strongly on component two. MOT loads most strongly on component one but there is evidence for some cross loading with component two.

In order to confirm that the structure described by the factor analysis was consistent when considering only the new sample, I examined the zero-order correlations between each of the variables (Table 5.4). The relationships observed in the factor analysis and in the regressions of Chapter 4 were replicated in the new sample, including the significant, positive correlations between subitizing, MOT and change blindness as well as correlations between the complex span tasks.

Subitizing	1						
CB	.35*	1					
MOT	.39*	.44*	1				
OSPAN	.17	.24	.25	1			
RSPAN	.08	.38*	.22	.47*	1		
SSPAN	-.03	.10	.19	.41*	.29	1	
Estimation	-.04	.18	.09	.01	-.08	.08	1
	Subitizing	CB	MOT	OSPAN	RSPAN	SSPAN	Estimation

Table 5.4 Pearson correlation matrix of behavioural variables for the sample of chapter five (n = 44; an asterisk denotes correlations significant at a threshold of p<.05). Note that CB represents detection sensitivity in the change blindness task.

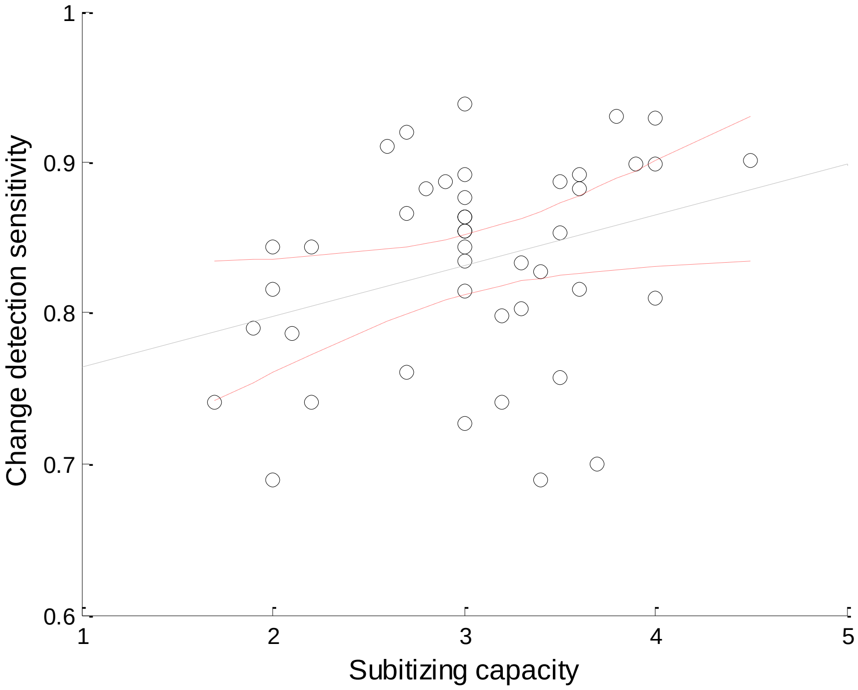

Figure 5.4 Scatterplot of the correlation between subitizing capacity and change detection sensitivity (red dashed line shows 95% confidence intervals).

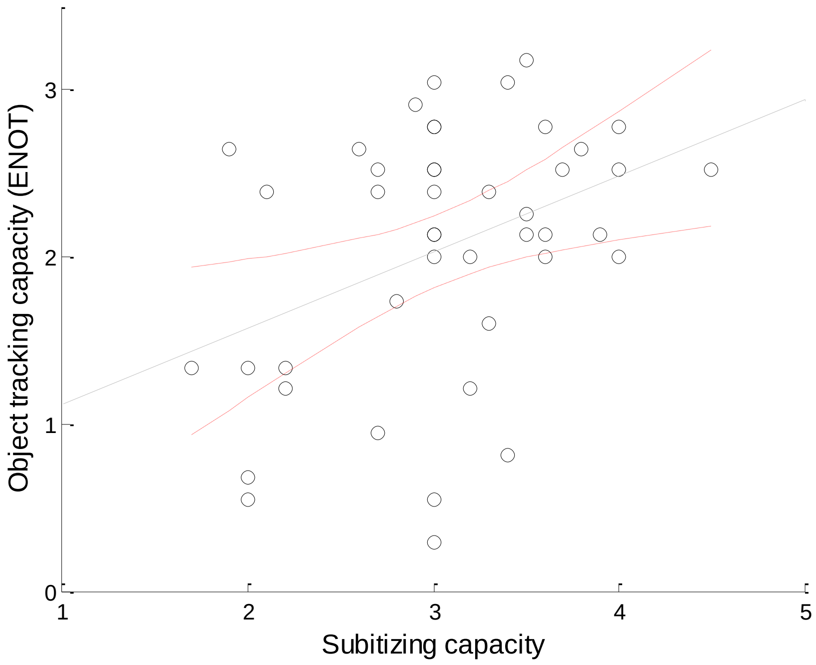

Figure 5.5 Scatterplot of the correlation between subitizing capacity and tracking capacity (ENOT) in the MOT task (red dashed lines represent 95% confidence intervals).

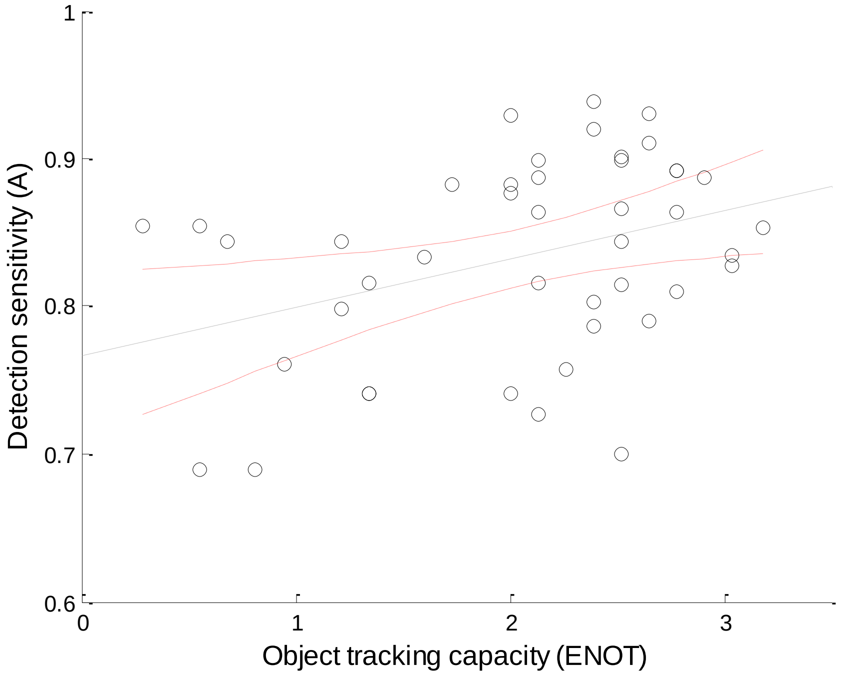

Figure 5.6 Scatterplot of the correlation between object tracking capacity (ENOT) and change blindness detection sensitivity (red dashed line displays 95% confidence intervals).

5.4 VBM analysis of MRI and behavioural data

All statistical analyses controlled for total intracranial volume (TIV), calculated as the total volume accounted for by grey matter, white matter and cerebrospinal fluid (CSF) for each participant. Analyses were constrained to grey and white matter separately by applying optimized masks generated using the masking toolbox developed by Ridgway et al. (2009), downloaded from: http://www0.cs.ucl.ac.uk/staff/g.ridgway/masking.

Multiple regression analyses were conducted on the pre-processed images in SPM12 to investigate the relationship between behavioural predictors and voxel-wise intensity values. A statistical threshold of $p <.05$ was employed, correcting for the whole image volume at the cluster level using non-stationary cluster extent correction. Non-stationarity correction is recommended for VBM analyses (Hayasaka et al. 2004), and this approach is widely employed in contemporary literature (e.g. Konstantinou, Constantinidou & Kanai, 2017; Chamberlain et al. 2014).

5.4.1 VBM correlates of subitizing capacity

First, subitizing was used as a predictor of grey matter to identify brain regions in which grey matter density is associated with greater subitizing capacity. This analysis revealed a significant, positive correlation in the TPJ of the right parietal cortex ($p < .001$ corrected for the whole grey matter volume; cluster size = 130 voxels; peak MNI coordinates: $x = 39$, $y = -66$, $z = 33$; Figure 5.7).

A further analysis which included estimation accuracy as a covariate to control for variance not specifically related to perceptual capacity revealed the same significant cluster which was unchanged. Further analysis showed that the correlation remained significant when controlling for complex span scores as covariates in place of estimation accuracy. No correlation reached significance between estimation accuracy and grey matter density whether or not subitizing capacity was controlled (p >.05 corrected for the whole volume).

Subitizing capacity is therefore significantly correlated with grey matter density in a region of the right parietal cortex. This relationship cannot be attributed to general cognitive performance or working memory capacity as both were controlled in analyses including estimation and complex span scores respectively.

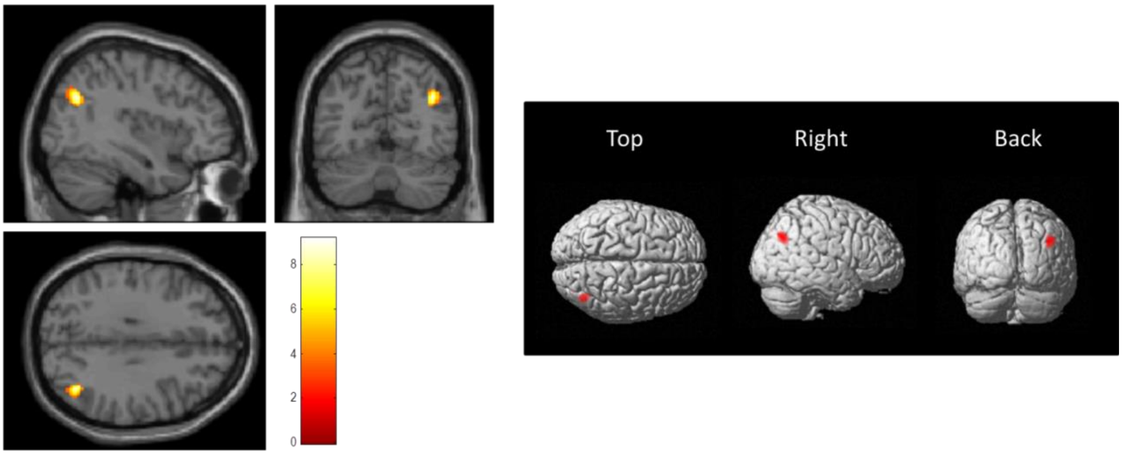

Figure 5.7 Results of VBM analysis with subitizing as a predictor of grey matter, showing a significant area of correlation in the right parietal cortex.

5.4.2 VBM correlates of change detection

The next VBM analysis used change blindness detection sensitivity as a predictor of grey matter density. This analysis revealed two significant clusters of positive correlation, one in the right parietal cortex – slightly anterior to the cluster associated with subitizing; and the other in the left medial prefrontal cortex, incorporating the anterior cingulate (Figure 5.8, Table 5.5).

A further analysis was conducted which included each of the complex span scores as covariates (as in the analysis of subitizing capacity) in order to control for any role of executive working memory in the effect. The parietal cluster remained significant with complex span scores as covariates but the frontal cluster was no longer significant.

Thus, it appears that both parietal and frontal cortical structures underlie visual change detection in the flicker paradigm. The fact that the anterior cingulate/ frontal cluster was no longer significant when controlling for working memory span implies that this correlation is related to the role of working memory in change detection. As the parietal cluster remained significant when working memory was controlled it appears that this relationship is not related to executive working memory but rather (given the previous results) with perceptual capacity.

Location	**Coordinates**			**Cluster size**	**P(corr)**	**P(uncorr)**
	x	y	z			
Anterior cingulate	-11	44	3	1732	.01	.003
Right TPJ	47	-60	36	745	.01	.002

Table 5.5 VBM results with change blindness as a predictor of grey matter

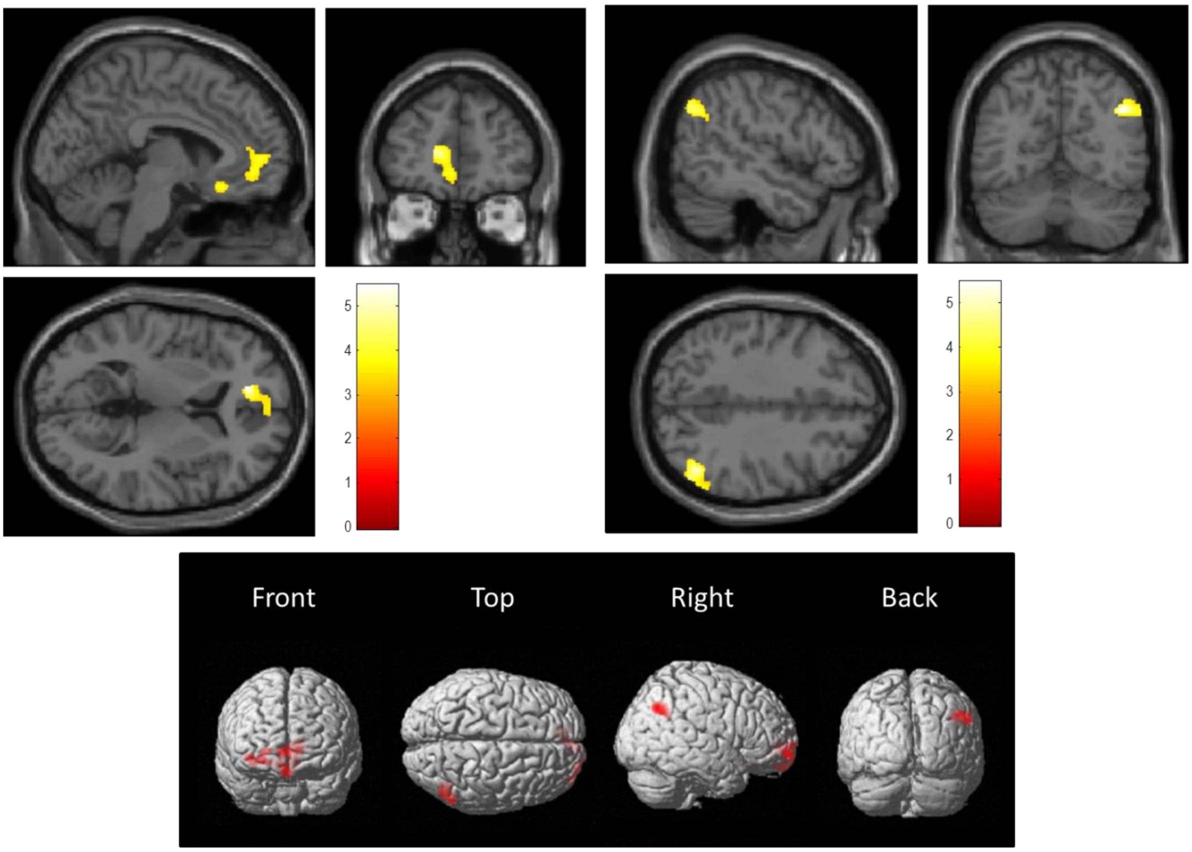

Figure 5.8 Results of VBM analysis with change detection sensitivity as a predictor of regional grey matter density. The upper right shows the cluster in Anterior cingulate and the upper left shows the right parietal cluster.

5.4.3 VBM correlates of MOT performance

Object tracking capacity was not associated with any statistically significant clusters in grey matter density anywhere in the brain.

5.4.4 VBM correlates of Complex span

To investigate the brain structures underlying complex span scores, a VBM analysis was conducted which included all three scores (OSPAN, RSPAN and SSPAN). A contrast which combined all three scores as predictors in conjunction was positively correlated with grey matter density in a significant cluster of the left middle frontal gyrus ($p = .005$, corrected for the whole grey matter volume; cluster size = 51 voxels; coordinates: x = -41, y = 20, z = 41; Figure 5.9). There was no significant correlation between grey matter density and any individual score independently.

These results suggest that the core capacity measured by the various complex span tasks (i.e. executive working memory) is chiefly associated with frontal cortical grey matter as has been proposed by various theories supported by functional imaging and clinical research. Indeed the left medial frontal cortex has previously been implicated in top-down suppression of distractor processing (De Fockert et al. 2004) as well as dual-task demands during complex span tasks (Chein, Moore & Conway, 2011). Despite involving different computational modalities (numerical/ lexical/ spatial), the separate tasks do not correlate specifically with individual brain structures.

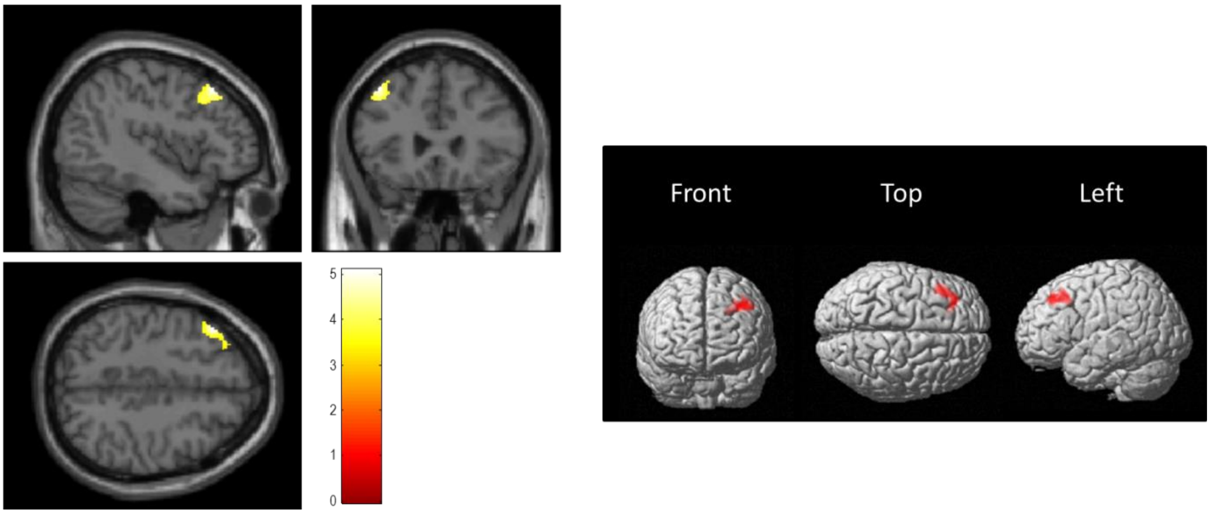

Figure 5.9 Results of a VBM analysis with OSPAN, RSPAN and SSPAN as predictors of regional grey matter density in conjunction

5.4.5 VBM correlates of general perceptual capacity

The final analysis was intended to establish whether a common area of grey matter would be associated with the general perceptual capacity hypothesised to underlie all three tasks. To achieve this, I conducted an analysis in which all three ‘perceptual’ variables (subitizing, change blindness and MOT) were used as predictors in conjunction. At the same time complex span scores were included as covariates to control for variance not associated with perceptual capacity.

There was one cluster of significant correlation when all three variables (subitizing, change blindness and MOT) were used as predictors (Table 5.6). This was located the right parietal cortex (p = .005; cluster size = 29 voxels; coordinates: x = 45, y = -63, z = 35; i.e. the region associated with subitizing and change blindness independently in the prior analyses). When any one of the scores was used as a predictor alone (e.g. when subitizing was a predictor and change blindness and MOT were covariates along with span scores) there was no significant correlation, indicating that the individual tasks were not associated with separate grey matter correlates. Instead the parietal cluster associated with change blindness and subitizing appears to represent the same underlying relationship. The parietal grey matter correlates of change blindness and subitizing may therefore underlie the common perceptual capacity resource suggested by the prior behavioural results.

Location	**Coordinates**			**Cluster size**	**P(corr)**	**P(uncorr)**
	x	y	z			
Right parietal cortex	45	-63	35	29	.005	<.001

Table 5.6 VBM results with subitizing, change blindness and MOT scores in conjunction while controlling for complex span scores.

5.5 Chapter conclusions

The behavioural results expand on those of Chapter 4, further supporting the concept of a general perceptual capacity as a distinct construct underlying performance in situations which load perception. Results of the PCA indicated two separate, orthogonal factors representing executive and perceptual variables. Thus subitizing, change blindness and MOT are all shown to share common variance which cannot be explained by working memory capacity or general factors. Furthermore, the results of the VBM analyses presented in this chapter extend this concept to neuro-anatomy, identifying distinct correlates of both perceptual and executive capacities in regional grey matter density. These results extend those of previous functional imaging investigations by providing insight into the structures associated specifically with individual differences, rather than simply areas active during task performance.

Subitizing capacity was correlated with voxel-wise intensity in a cluster of the right TPJ. This relationship remained significant when controlling for variance related to general cognitive effort and working memory capacity by including estimation accuracy and complex span scores as covariates. The right TPJ has previously been implicated in subitizing with studies using functional MRI (Vetter et al. 2011) and structural comparisons of lesion patients and controls (Demeyere, Rotshtein & Humphreys, 2012) have implicated the right parietal cortex generally. Other measures of perceptual capacity have been linked to parietal cortex (MOT: Jovicich et al. 2001; Culham et al. 2001) and in particular the right TPJ (VSTM: Todd et al. 2005). The present results confirm that right parietal grey matter density is associated with subitizing capacity among healthy individuals, even while controlling for non-perceptual processing resources.

Similarly, change blindness was associated with grey matter density in approximately the same region of right parietal cortex as well as in medial prefrontal cortex. As was found with subitizing capacity, the right parietal cluster associated with change detection remained significant when controlling for working memory capacity; whereas the cingulate cluster was no longer significant. As discussed in the chapter introduction, right parietal activity has been established to play a causal role within change blindness tasks along with right frontal and category specific visual areas (Beck et al. 2001; 2005). The present results establish novel evidence that individual differences in change blindness are associated with right parietal and medial frontal grey matter density. Furthermore only the frontal correlation can be accounted for by executive working memory, in line with the well-established role of frontal cortex in executive functions (e.g. Chein et al. 2011).

Tracking performance in the MOT task did not reveal any significant correlations with regional grey matter density. This is interesting, as behavioural performance of the task was consistently associated with the other perceptual tasks. Prior neuroimaging evidence has established widespread activations within parietal and frontal cortices is increased by tracking and related to tracking load as well as in higher visual cortex and even the cerebellum (e.g. Culham et al. 2001; Jovicich et al. 2001; Jahn et al. 2012). The prior evidence would therefore appear to indicate that widely distributed networks of areas are involved in MOT performance, possibly indicating contributions from multiple cognitive resources. This is corroborated by the behavioural results of both this and the previous chapter; which indicated that both perceptual and working memory capacity contribute to individual differences in MOT performance. It is therefore possible that no one of these brain functions was the sole determinant of any individual’s maximum tracking capacity. That is, the MOT task does not represent a ‘pure’ measure of perceptual capacity, but rather performance can be compensated by other cognitive resources.

Complex span working memory capacity was associated with a significant cluster of the left middle frontal gyrus. This relationship was significant when all span scores were used in conjunction, and there was no significant regional correlation specific to one independent memory span task. Thus it appears that the significant cluster in the present results is associated with the executive component of the working memory tasks as opposed to any domain-specific processing or memory storage. Complex span tasks have been associated with functional activity in the lateral prefrontal cortex, along with the anterior cingulate and posterior parietal cortices, in previous research (Chein et al. 2011; Osaka et al. 2003). Importantly, Chein and colleagues demonstrated that activity in these regions is specific to the domain general executive control aspects of complex span rather than any specific memory storage component of the tasks. In the present results, individual differences in complex span are associated only with the left middle frontal gyrus, indicating that this structure may be a key factor in establishing individual's working memory performance. In parietal cortex there was no significant association with complex span in the present results, nor did the inclusion of span scores account for parietal correlates in the subitizing or change blindness tasks. This suggests that although parietal cortical processing is recruited in performing complex span tasks, this area is not critical to individual differences in executive control of working memory.

In the final analysis, the same region of parietal cortex was associated with the conjunction of all 'perceptual' variables, when controlling for working memory capacity. Likewise, the lateral frontal cluster was correlated with the conjunction of working memory scores while controlling for perceptual capacity. No individual behavioural measure accounted for significant unique variance in any region of grey matter when controlling for all of the others. Thus, the evidence from this chapter supports the conclusion that distinct constructs of perceptual and executive capacities, which apply to a variety of behavioural tasks, can be dissociated at the neuroanatomical level.

Chapter 6

General discussion

6.1 Overview of findings

The research reported in this thesis established individual differences in perceptual capacity which underlie awareness and performance in attention demanding situations. Chapter 2 established that distractor interference effects are dependent upon subitizing capacity in a visual enumeration task. Distractors caused significant detriment to accuracy (Experiment 1) and reaction times (Experiment 2) within the subitizing range but not beyond. Furthermore the effects of distractors were sensitive to individual differences: Individuals with greater subitizing capacity were susceptible to distraction at higher set sizes than were those with lesser capacity. In conjunction with previous literature demonstrating parallels between perceptual load and subitizing effects, these findings supported the use of subitizing as a measure of individual perceptual capacity in subsequent experiments.

Having established the subitizing range as a measure of perceptual capacity, I then investigated common variance between diverse measures of perceptual and non-perceptual processing. The results showed that subitizing capacity is a significant predictor of detection rates and detection sensitivity in inattentional blindness paradigms (load-induced blindness in Chapter 3 and change blindness in chapters 3-5). The relationship between subitizing and awareness in these paradigms was specific to the subitizing range and could not be explained by performance in numerical estimation of supra-subitizing sets. I then confirmed that this common variance underlies subitizing, MOT and change blindness while being distinct from higher cognitive working memory capacity. These results further support the concept as proposed by load theory that working memory and perceptual capacities are distinct constructs with contrasting roles in perceptual processing.

In addition, distinct correlates of perceptual and working memory capacity were found in regional grey matter density. The right TPJ was associated with subitizing capacity as well as change detection sensitivity whereas working memory capacity was associated instead with a region of left frontal cortex. These correlations remained significant when using various other tasks as control variables, indicating that the underlying relationships are specific to perceptual and executive capacities respectively.

6.2 Evidence for a general perceptual capacity

The results reported throughout this thesis are consistent with a limited perceptual capacity, common generally to tasks involving perceptual load and distinct from higher level cognitive control resources. Previous research has indicated that perceptual load determines distractor processing, stimulus detection and inattentional blindness phenomena. However, until now it has been unclear whether common perceptual resources underlie all of these effects. By employing an individual differences approach the present results provide evidence for common resources shared across these paradigms while also extending the load theory framework to visual enumeration.

The limits on subitizing have been proposed to represent a capacity limit for indexing or individuating multiple stimuli in parallel (Trick & Pylyshyn, 1993; 1994; Mazza & Caramazza, 2015). This capacity limit is thought to apply to any task which requires attentional selection of multiple distinct stimuli at once. However, some recent research has shown that manipulations of perceptual load which do not involve parallel individuation of multiple stimuli still lead to impaired subitizing performance (Vetter et al. 2008; Burr et al. 2010, see section 1.3.4.1 of the General Introduction). These findings indicate that the capacity limit underlying subitizing can be loaded not only by increased number of items, but also by increased perceptual complexity of a concurrent task. In this thesis I proposed that this capacity limit is the same as the perceptual capacity limit described in load theory, and is therefore common to any task involving perceptual load.

The results supported this hypothesis: individual differences in subitizing capacity were consistently and uniquely related to perceptual load effects in diverse paradigms. In Chapter 2 processing of distractor stimuli was only found within the subitizing range and was eliminated when subitizing capacity was exhausted. This result parallels the results frequently reported in load theory literature, wherein distractor stimuli are involuntarily processed within capacity but effectively filtered when capacity is exhausted by increased load. The capacity represented by subitizing is therefore not related only to voluntary selection of targets, but is also subject to spill-over to irrelevant distractors as predicted by load theory. Subsequent chapters then demonstrated that the capacity underlying subitizing is important for a more diverse range of demands than enumeration of simple shapes. Rather, a variety of task demands and stimulus features were found to share a common underlying resource; providing further support for the hypothesis that perceptual capacity is a general and flexible resource.

The results are therefore largely in agreement with load theory, which predicts that perceptual capacity should be an important factor in any task involving high perceptual load, including situations of inattentional blindness. Subitizing was a significant predictor of detection sensitivity in both the change blindness and load-induced blindness paradigms. Furthermore, in both cases the relationship was specific to subitizing as it remained significant when controlling for performance in higher set size enumeration. As mentioned, a distinct cognitive resource is thought to underlie estimation of larger sets, one which may not require attentional resources (e.g. Burr et al. 2010). Despite this, all aspects of the enumeration task used throughout chapters 3, 4 and 5 were identical whether participants were subitizing or estimating numerosity. Both aspects of the task required detection of multiple objects and immediate report of their number. The ‘subitized’ and ‘estimated’ displays were presented in randomly intermixed order; indeed any given display may be subitized by one participant but estimated by another depending on their capacity. Thus factors relating to motivation, strategy, or cognitive resources other than perceptual capacity should play a similar role in both subitizing and estimation measures. The only distinguishing factor is the underlying cognitive resource, which, in the case of subitizing appears to be a significant predictor of subjective blindness in line with the predictions of load theory.

The generality of perceptual capacity was further attested to by the common variance with MOT performance, which involves very distinct demands compared to the subitizing and stimulus detection paradigms. However, MOT also had a unique relationship with executive working memory capacity, as demonstrated by significant direct relationships between these variables in Chapter 4 and by the cross-loading of MOT in the factor analysis of Chapter 5. Effective performance of the MOT task requires participants to maintain attention to the individuated targets over a relatively long period of time (eight seconds in the paradigm used here). Executive control may therefore be necessary to sustain appropriate allocation of perceptual resources to targets over the extended period, thus explaining the complimentary roles of both executive working memory and perceptual capacity. In previous research, executive working memory capacity was not significantly associated with MOT performance when controlling for shared variance with VSTM capacity (Trick et al. 2012). Although the present results would appear to contradict this finding, VSTM is not a pure measure of perceptual capacity but also involves top-down control for filtering relevant and irrelevant stimuli (e.g. Fukuda & Vogel, 2009, see General Introduction section 1.4.1). The shared role of executive control may therefore be similar in both VSTM and MOT tasks, explaining why it is a significant predictor but not when controlling for VSTM.

Further evidence that this capacity is specific to perceptual processing comes from the distinct variance attributed to working memory capacity in chapters 4 and 5. Working memory is a very diversely influential construct which plays a significant role in performance of all manner of tasks, including visual attention paradigms (Kane et al. 2001; Redick & Engle, 2006). Load on working memory resources has repeatedly been shown to have contrasting effects to those of perceptual load in both behavioural performance and brain activity (e.g. Lavie et al. 2004; De Fockert, 2013). This distinction is further supported by the results observed in chapters 4 and 5 of this thesis. In these results, tasks involving high levels of working memory load represented distinct behavioural variance to those involving perceptual load, and these tasks were associated with different neural correlates. The present individual differences results therefore compliment previous experimental research: Perceptual capacity appears represents a distinct cognitive construct from working memory, specific to perceptual processing and common to diverse sources of perceptual load.

Interestingly, in chapters 3 and 4, estimation accuracy was a significant unique predictor of change blindness alongside subitizing and working memory. As discussed in the General Introduction, recent models of visual enumeration describe numerosity as a basic visual feature (Burr & Ross, 2008; Anobile, Cicchini & Burr, 2016). This is thought to provide a mechanism by which numerosity can be perceived without direct attentional selection of individual items, explaining the fact that estimation ability is retained in situations where attention is not available (e.g. Burr et al. 2010; 2011; see General Introduction section 1.3.4.1). In a parallel line of research, perception of summary statistics representing basic visual features such as colour, orientation and size have been suggested not to require direct attention in a similar fashion (e.g. Alvarez & Oliva, 2008). These perceptual summary statistics have been proposed to underlie ‘gist’ perception from complex natural scenes, thereby providing a possible means by which estimation could share unique variance with change detection (e.g. Ward, Bear & Scholl, 2016, Rensink, 2004). Testing this hypothesis is beyond the scope of this thesis, for which the focus is on perceptual capacity and subitizing. Nevertheless the results of chapters 4 and 5 support the conclusion that estimation represents a process distinct from subitizing, which serves to further specify the boundary of perceptual capacity.

6.3 Implications for load theory

As discussed in the General Introduction, previous research has established that averaged across a typical sample, perceptual load effects are only observed with search set sizes of four items or more (e.g. Lavie & Fox, 1997; Lavie & Cox, 2000; Remington et al. 2009). There is some evidence that perceptual capacity can vary in special populations such as individuals with Autism or experts in a particular stimulus category (Remington et al. 2009; 2012; Baylis & Kritikos, 2011; Ro et al. 2009). However, these special cases have limited generalizability to the wider population. Previous research also fell short of providing a means of measuring the specific capacity limit for a given individual – rather, they established that larger manipulations of load were necessary to exhaust capacity when averaged across samples.

The 'intermediate load' designs used in previous literature are of limited utility in determining precise capacity limits, especially for individual participants, because they are reliant on an interaction between the effects of load and distractor condition. Because load is defined in these paradigms by its effect on distractor processing it is difficult to measure load (and therefore capacity) outside of this effect. The enumeration paradigm provides a means of circumventing this problem. The subitizing range is measured directly from enumeration accuracy (or response times) by identifying the point at which performance transitions from a flat to a negative slope (or a positive slope in the case of response time). By combining the enumeration and distractor interference paradigms in Chapter 2 I was able to establish that not only is distractor interference eliminated by increased load beyond four items (as in previous literature); but also that the effect of distractors on performance is dependent upon individual subitizing capacity as measured directly from enumeration performance.

The results reported in Chapter 2 therefore provide novel evidence in support of perceptual capacity as conceptualised in load theory. Despite being entirely irrelevant to the task and despite participants being instructed to ignore them, distractors still caused significant interference in task performance, but only within the subitizing range. This is in accordance with the load theory proposal that perceptual processing will proceed automatically and unavoidably within perceptual capacity limits and be eliminated when capacity is exhausted. Most importantly, distractor interference was eliminated by set sizes of three or more items for the lowest capacity participants whereas the highest capacity participants were still distracted when enumerating sets of three and four. This result establishes that perceptual capacity and the effects of perceptual load are subject to inter-individual variability. Furthermore, this also further validates the conclusion that perceptual capacity (and subitizing) represents a distinct construct from higher-level cognitive control. Working memory load has consistently been shown to have opposite effects to those of perceptual load (e.g. Lavie et al. 2004; De Fockert, 2013; see section 1.2.2 of the General Introduction) and individuals with lesser executive working memory capacity have been shown to be more susceptible to distraction than higher capacity individuals (Ahmed & De Fockert, 2012). Therefore, if top-down cognitive control resources underlie subitizing then individuals with greater subitizing capacity would be expected to have reduced susceptibility to distraction. This is the opposite result to that reported Chapter 2, in which higher capacity participants were more susceptible to distractors.

6.3.1 Insights to load theory from an individual differences perspective

Paradigms used to establish load effects on detection (i.e. load-induced blindness) typically involve the participant directing their attention toward a central task while also attempting to detect the occasional appearance of peripheral stimuli (see General Introduction, section 1.2.1). The conclusion drawn from results of these studies is that as the central task consumes more perceptual capacity less capacity is available to allocate to the detection of peripheral targets. However, an alternative explanation is that the increased difficulty under high load incentivised participants to exert greater attentional suppression to the non-target stimulus locations. This is supported by findings suggesting that the effects of perceptual load are not uniform across the visual display. Instead, increased perceptual load has been associated with an increased suppression of processing in the immediate periphery of the attended task which tapers off with increased distance, forming a ‘Mexican hat’ distribution of distractor suppression (Linnell & Caparos, 2013; Ahmed & De Fockert, 2012). According to this interpretation, perceptual load leads to inattentional blindness not because perceptual capacity has been exhausted but rather because peripheral targets fall in the area of suppressed processing. This interpretation is not easily reconcilable with phenomena such as subitizing, and would imply that the effects of perceptual load and subitizing capacity are unrelated. The top-down suppression account of perceptual load would not therefore predict any relationship between subitizing capacity and detection sensitivity in subjective blindness tasks; contrary to the results observed here.

The results also establish that the role of perceptual capacity cannot be attributed to dual-task elements present in load-induced blindness paradigms. Apart from the load-induced blindness task, all the other tasks used here involved only one objective, and shared variance in performance across these tasks was the measure of interest. In contrast, previous research manipulated secondary task load to establish the role of load in awareness. That is, previous paradigms have required participants to direct their attention toward a central visual search or discrimination task of high or low load, while also detecting changes to images presented in the periphery or background (e.g. Beck et al. 2001). In the results presented here however the change blindness paradigm did not involve any dual-task element, instead participants were able to direct their attention solely to the detection of changes. Still, perceptual capacity was a significant and unique predictor of participant's detection ability. This is important in that it demonstrates that even when the observer is not required to split their attentional resources between the two displays, perceptual capacity is still important for change detection.

The change blindness paradigm involved complex real-world scenes, with flickering displays designed to eliminate 'pop out' of the target (change) stimulus. Thus the task constitutes a type of visual search involving high perceptual load, sufficient to exhaust capacity and elicit 'blindness' at least temporarily in nearly all observers. This necessitates a slow and serial search of the image, selecting individual components and checking whether or not they change from image to image. It is conceivable, therefore, that individual differences in perceptual capacity would play no important role in such a task. If the level of load is sufficient to exhaust the capacity of any observer, then this might equate all observers, as even those with the highest capacity must resort to systematic and serial search of the image, one component at a time. Instead, the key factor in determining change detection would be the effectiveness in organising one's search, ensuring that one does not revisit the same image component unnecessarily (i.e. cognitive control). This was not the case in the results reported here; instead perceptual capacity as measured by both subitizing and MOT was consistently a significant predictor of change detection, even when controlling for top-down control resources. This result instead implies that participants with greater capacity are able to select more information from the image at once, thus increasing the chance that on a given presentation ('flicker') they will select the correct item or location and notice the change.

The diversity of the paradigms sharing common variance attests to the generality of perceptual capacity. While, as described, the change blindness task involved repeated presentations of complex real world scenes; the load-induced blindness task involved relatively simple and abstract stimuli in which participants split their attention between two task demands. The enumeration and MOT tasks both involved selection of several stimuli in parallel but in very different task contexts, the enumeration task involved rapid selection and response and the MOT task involved continued selection for extended periods. Nonetheless, across all of these tasks the results converged to indicate a common underlying resource. As predicted by load theory, perceptual capacity appears to be an important construct in performance under diverse sources of perceptual load. Also in line with the predictions of load theory, this capacity was consistently shown to be distinct from working memory capacity in both behavioural and neuroimaging results (discussed next).

6.4 Load and individual differences in brain morphology

Previous neuroimaging research has demonstrated effects of perceptual load in category specific cortical processing (Rees et al. 1997) and at very early stages of perceptual processing (e.g. Schwartz et al. 2005). The distinction between perceptual and cognitive load has also been supported by neuroimaging evidence (De Fockert et al. 2001; Kelley & Lavie, 2010). However, these investigations have been uninformative regarding the role of individual differences in the effects of load.

The question therefore remained as to the area of cortical processing at which individual capacity limits are realized. Effects of individual differences in perceptual capacity on primary visual cortex could imply that greater representational capacity in these early cortical regions would facilitate greater perceptual performance. Alternatively, the limits of perceptual capacity may be realized at somewhat higher levels of processing as suggested by cross-modal effects of load (e.g. MacDonald & Lavie, 2011; Dalton & Fraenkel, 2012) and the linear effects of load in parietal activity (e.g. Culham et al. 2001, Torralbo, Kelley, Rees & Lavie 2016). Still other accounts, which argue against the load-theory proposition of a perceptual capacity limit, might suggest that the effects of load are related to top-down activity originating at the highest level of prefrontal cortical processing (e.g. Benoni & Tsal, 2013).

The results of Chapter 5 provide some insight regarding this question. VBM analysis provides a means of measuring individual differences in grey matter volume throughout the brain while controlling for confounds such as overall brain size and differences in gross cortical arrangement. The image intensity at a given location therefore provides a measure of cortical grey matter density for each individual, which can be correlated with behavioural measures. In Chapter 5, VBM analysis was used to explicitly investigate the brain structures underlying perceptual and working memory capacity limits. This approach was therefore able to identify the brain regions associated with capacity per se, as opposed to the regions active during task performance. The results indicated that perceptual capacity is associated with regional differences in right parietal cortex, specifically the TPJ. In contrast, the capacity of executive working memory was correlated with grey matter density in the left frontal cortex. Thus, although the functional effects of load can be detected at very early stages of perceptual processing, these effects appear to depend in some way on processing in the right TPJ. Approximately the same cortical area was associated with both change detection sensitivity and subitizing capacity, and both of these relationships withstood controls for non-perceptual working memory capacity. However, in analyses using all behavioural variables in conjunction, no individual task accounted for significant unique variance. It therefore appears that the relationships of right parietal grey matter with both subitizing and change blindness represent the same underlying construct.

Whereas subitizing capacity was associated only with a single cluster in right parietal cortex, change detection sensitivity was also associated with a cluster incorporating anterior cingulate and prefrontal cortex. Interestingly, the parietal cluster remained significant in both tasks when controlling for working memory capacity, but the frontal correlates of change detection were no longer significant. This is interesting because change blindness was not significantly associated with any of the working memory capacity measures in either Chapter 4 or Chapter 5. It appears however, that inter-individual variance in frontal grey matter density is common to performance of both tasks. As discussed earlier, the change blindness flicker paradigm constitutes a task with high perceptual load, and therefore an inefficient visual search (Roper et al. 2013; Wolfe, 2007). Such inefficient search would require top-down organisation in order to avoid re-visiting previously searched image components and perform optimally. It is therefore logical that top-down control processes associated with prefrontal cortex would be involved in performance in this task. This observation further points toward the right TPJ as the key location in perceptual capacity, as well as indicating that subitizing represents a particularly pure measure of this capacity.

The right TPJ has frequently been implicated in attentional orienting and spatial attention in previous functional imaging investigations. Neuropsychological studies have also shown that damage to this area can result in contralateral neglect of sensory information (e.g. Friedrich, Egly, Rafal & Beck, 1998). This further supports the existence of a capacity for perceptual processing which is common to perceptual tasks in general and is essential for conscious awareness of visual stimuli. Functional imaging research has also associated activity in the right parietal cortex with subitizing. For example, Vetter et al. (2011) manipulated the perceptual load of a central task while participants simultaneously attempted to enumerate surrounding stimuli. The behavioural results of this paradigm in similar studies established that perceptual load significantly impairs subitizing performance but not larger number estimation (e.g. Vetter et al. 2008; Burr et al. 2011; See section 1.3.4.1 of the General Introduction). In their fMRI study, Vetter et al. (2011) found that activity in the right TPJ was modulated by load within the subitizing range but not by larger sets. These findings provide evidence that activity in the TPJ underlies processing within perceptual capacity. When perceptual capacity limits are reached, activity in the TPJ reaches its ceiling and cannot therefore increase further with additional load. Furthermore, activity in the right TPJ has also been shown to be negatively associated with VSTM load, but only within behavioural capacity limits of up to four items (Todd et al. 2005). Todd and colleagues also showed that VSTM load results in inattentional blindness, suggesting that processing limitations in the TPJ are the source of VSTM and perceptual limitations. In conjunction with previous literature, these results appear to indicate that the capacity limit underlying general perceptual processing is localized to the right TPJ and that this is distinct from higher level working memory capacity which is associated with frontal cortex.

Results of prior neuroimaging studies have also established opposite effects of cognitive and perceptual load in parallel to the contrasting behavioural effects. Whereas increased perceptual load leads to significantly reduced distractor and target-related activity in early sensory cortices (e.g. Rees et al. 1997); cognitive load has been shown to significantly increase this activity (De Fockert et al. 2001; Kelley & Lavie, 2010). In the results I present in Chapter 5, working memory capacity is associated with lateral cortical grey matter density in the left frontal lobe. The frontal cortex in general has long been associated with top-down cognitive control, and indeed previous research has shown that complex span tasks specifically recruit activity in frontal cortex. For example, Osaka et al. (2003) administered a listening span task to participants during fMRI; their task was comparable to the complex span tasks used here: Participants listened to a sentence, memorized the first word and simultaneously indicated whether or not the sentence made sense (as in the RSPAN task used in chapters 4 and 5). In their investigation, memory task performance increased activity in the superior temporal gyrus, anterior cingulate and importantly the left middle and inferior prefrontal cortex. A more recent investigation by Chein et al. (2011) reported similar findings using complex span tasks with both spatial and verbal memoranda. They found that activity in the lateral prefrontal, anterior cingulate and posterior parietal cortices were each significantly modulated by complex span working memory tasks. These authors concluded that domain general control of attention primarily involves the frontal and anterior cingulate cortices. In both of these studies the locus of activity in the frontal cortex included the same area of significant correlation reported in Chapter 5. Thus, the left lateral frontal cortex appears to be a key limiting factor in determining individual working memory capacity limits. This result also fits well with the results of a previous investigation of activity evoked by distractor processing in a study by De Fockert et al. (2004). In this study, participants searched for a visual target stimulus while ignoring irrelevant colour singletons. The authors reported that activity in bilateral parietal cortex as well as the left frontal cortex was associated with attentional capture by task-irrelevant distractor stimuli. Importantly, the level of activity in frontal cortex was negatively correlated with the behavioural interference effect caused by the distractor. That is, distractor interference was reduced on trials with greater frontal cortical activity. The distractor-related activity in parietal and frontal cortices appears to represent bottom-up capture and top-down control processes respectively. Thus, the results presented here confirm previous literature in establishing distinct correlates of perceptual and executive capacities in the brain.

6.5 Future research and applications

Building on previous literature, the results reported in this thesis support the load theory hypothesis of a task-general limited-capacity resource, one which is distinct from the capacity for working memory or cognitive control. Furthermore, perceptual capacity limits have consistently been shown to vary from individual to individual, contributing important variance to performance in diverse visual attention tasks. As discussed above, it has long been established that individuals vary considerably in their capacity for top-down cognitive control, and this inter-individual variability has been shown to play a significant role in performance of various tasks. While researchers often take into account the role of individual differences in working memory capacity when interpreting their results, this is less often the case with perceptual capacity. Future research may therefore benefit by including subitizing or a similar task as a measure of participant's perceptual capacity limits. This could provide additional insight to experimental results, especially with regard to load theory research in which arbitrarily defined 'high' and 'low' load conditions are administered to a sample, or when samples are compared in terms of load effects. By incorporating an individual differences perspective, load theory research could fruitfully explore how load and capacity interact in determining load effects.

There is evidence that subitizing capacity, as well as MOT, may benefit from cognitive training, especially through action video-game play (Green & Bavelier, 2006). In their influential study, Green and Bavlier found that the subitizing and tracking capacities of video game players were enhanced relative to non-game-playing controls. Furthermore, an intervention involving ten hours of video game play over fifteen days was found to significantly increase the capacities of non-players. This result has been replicated in subsequent investigations which demonstrated that action video games imparted significant advantages over various controls. Expert action video-game players also have significantly greater grey matter density in right parietal cortex (Tanaka et al. 2013). So-called 'brain-training' is a contentious issue in contemporary cognitive research: studies investigating the effects of training interventions frequently find null effects, and the significant results that are reported appear to have limited replicability and limited transfer beyond the trained tasks (Shipstead, Redick & Engle, 2012; Melby-Lervåg, Redick & Hulme, 2016). These studies tend to focus on training executive functions and as demonstrated throughout this thesis, perceptual capacity represents a distinct construct from working memory or executive control. It is possible therefore that perceptual capacity may be more receptive to training effects, the task-general role of perceptual capacity as outlined in this thesis may explain the dichotomy between studies showing strong training effects and transfer (Green & Bavelier 2006) and those showing no training or narrow transfer (Melby-Lervåg et al. 2016). Future research on cognitive training effects may therefore benefit from applying the load theory framework to identify the target of training – perceptual capacity or working memory.

Finally, the results reported here demonstrate the importance of perceptual capacity in a variety of tasks which have relevance to real-world situations. Specifically, the ability to identify and track stimuli as well as to detect changes in complex real-world scenes is of clear importance to various security-related tasks. For example, personnel selected for security roles involving monitoring of visual information from CCTV, satellite and aerial images or x-ray luggage scans must perform challenging perceptual judgements on a regular basis. As demonstrated throughout this thesis, there is significant inter-individual variability in people's ability to perform these perceptual judgements. Therefore, the tasks used here as well as related paradigms provide potential means to identify participants who may perform these safety-critical tasks most effectively. Subitizing especially provides a relatively pure measure, as demonstrated by its consistent independence from other behavioural measures and brain structural correlates. The subitizing tasks used throughout this thesis are easily administered in only a few minutes on a standard computer, requiring little explanation to the participant and no specialist equipment. If combined with other measures, especially complimentary measures of cognitive control, subitizing capacity could provide a useful addition to testing batteries for personnel selection in various military and security roles involving high perceptual load.

6.6 Conclusion

In conclusion, the findings presented in this thesis provide evidence for a common perceptual capacity which underlies performance of perceptually demanding tasks. The generality of perceptual capacity is attested to by the diverse task demands and stimulus features across the tasks. In line with the load-theory hypothesis, a common resource appears to underlie subitizing, object tracking and stimulus detection in subjective blindness paradigms and the variance attributed to perceptual capacity was not explained by working memory or other cognitive resources. The dissociation between perceptual and cognitive control resources in terms of both behavioural variance and neuroanatomical correlates further supports the distinction between perceptual and working memory capacities. Overall the present results thus provide further support for the assertion that the capacities for perceptual processing and cognitive control are dissociable as predicted by load theory. These results thus support the load theory framework as a means of understanding performance limitations across diverse task demands. Furthermore, the results establish that individuals across the general population exhibit variability in their perceptual capacity which affects their performance in a variety of tasks. These findings establish the construct of perceptual capacity, relate attention research across broad domains and offer the potential for application as tests in applied settings. This thesis therefore has important implications for future research and for real-world applications.

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