VISUAL ENUMERATION AND ESTIMATION:

BRAIN MECHANISMS, ATTENTIONAL DEMANDS AND NUMBER REPRESENTATIONS.

by

NELE DEMEYERE

A thesis submitted to

The University of Birmingham

For the degree of

DOCTOR OF PHILOSOPHY

School of Psychology

College of Life and Environmental Sciences

The University of Birmingham

January 2010

ABSTRACT

The work presented in this thesis explored the roles of attention and number apprehension in visual enumeration and estimation through a variety of methods. First, a distinction was made between different attentional modes underlying estimation and enumeration in an in-depth single case study of a patient with simultanagnosia. Subsequently I demonstrated that, in visual enumeration, subitizing and counting are dissociable processes and they rely on different brain structures. This was done through a neuropsychological single case study as well as through the first large sample neuropsychological group study using a voxel-based correlation method. Following this, behavioural methods were used to examine the relations between subitizing and estimation. I found that, under conditions encouraging estimation, subitizing is an automatic process and may lead to the exact representation of small numbers, which contrasts with approximate representations for larger numerosities. Finally, a functional MRI study was conducted to highlight the brain regions that are activated for subitizable numerosities, but not for larger numerosities under distributed attention conditions. The imaging study provided converging evidence for automatic subitizing leading to an exact number representation. The last chapter discusses the implications of the contrast between subitization and counting for understanding numerical processing.

ACKNOWLEDGMENTS

It is hard to overstate my gratitude to my PhD supervisor, Professor Glyn Humphreys. Had I not met him, I doubt I would have undertaken a PhD. From when I was originally doing a research internship here as a Masters' student from Leuven, my experience working with Glyn can maybe best be described as eye-opening. His supervising style, humility and pragmatism struck a chord with me and even during that short time he transformed my understanding of research and made it fun and challenging. I could easily see myself doing more of this – and I shortly applied for a PhD with him. Glyn must be the busiest and most hard working person I have ever met, his drive and motivation is endless. Yet, amazingly, he always has time for you. His door is always open and I have always felt I could simply knock on his door for virtually any question. Despite collaborating and supervising with what seems like hundreds of people, within seconds of asking something, he is able to exactly recall what experiment you are talking about and grasp and place your question and give you that sensible answer that would have probably taken you a day to find out on your own. And you're out of there in 5 minutes. This makes for incredibly efficient work and is probably the reason why he is such a publications machine. For being such an authority in the field, Glyn is incredibly humble, and makes you feel as a collaborator, rather than a student. He has a contagious enthusiasm for results (you can always drop in with results!) and manages the incredible balance between gentle and firm guidance. I will probably never understand how he manages it all. My utmost thanks, I could not have wished for a better supervisor.

Special thanks also goes to Dr. Pia Rotshtein, without whom SPM would still be a secret to me. She always found time for me and my analyses and her inventiveness and insightful discussions have been very helpful.

Next, a big thank you to all participants in my studies; most notably the patients who feature prominently throughout this thesis. Special thanks goes to GK in particular, our weekly Monday morning meetings were most enjoyable, he was incredibly wise, with an immensely positive outlook on life and a great sense of humour. His motivation and his determination to overcome difficulties, were truly inspiring. He sadly suffered another stroke and passed away - I will always cherish those memories of Monday mornings with him.

There are a number of people in my everyday circle of fellow PhD students (and friends) who have enriched my PhD life in various ways. I would like to thank Noreen, Gemma, Sarah, Christine and Magda for their support and help at various stages of my PhD.

Last but not least, I thank my family, my parents for giving me the opportunity to study and encouraging me to pursue my interests; even when these went beyond our national borders. Thanks also to my sister for her love and support.

Most importantly, thank you to my husband, Phil, who has been the best supporter anyone could wish for. Thank you for all the practical support, including help with photoshop and scripting and being a stay-at-home dad looking after our little crazy monkey. But perhaps even more importantly, thank you for the invaluable moral support – you have the amazing ability to instil confidence in me and to make me laugh – even in the hardest times. I could not have done it without you.

Finally, thank you to my beautiful baby girl, Lotte, your smile and energy are incredibly contagious. You have changed my life.

TABLE OF CONTENTS

CHAPTER 6:

CHAPTER 7:

LIST OF ILLUSTRATIONS

LIST OF TABLES

CHAPTER 1:

INTRODUCTION

Visual Enumeration – Subitizing and counting

The time taken by people to count visual stimuli varies in a highly systematic fashion as a function of the number of stimuli present: reaction times (RTs) show only a small rise as the number of stimuli increases from 1 to 4 (typically at a rate of around 50-80 ms per item), while for larger numbers there is a slower and more clearly linear increase in RT for every item that is enumerated (typically increasing at a rate of about 200 ms/item) (Mandler & Shebo, 1982; Trick & Pylyshyn, 1993). This generates a characteristic 'dog leg' function, from a shallow to a steep enumeration slope (see Figure 1). The difference in the slope of the counting function for small (<4) and larger numbers (>4) has formed the basis for the theoretical distinction between "subitizing" (the ability to enumerate in a fast and accurate manner a small group of four or so objects) and "counting" (the more error prone and slow process of serially counting five objects and more). The term subitizing was first coined by Kaufman et al. (1949) and referred to a specific process distinct from other aspects of counting. It is this issue that is addressed in this thesis.

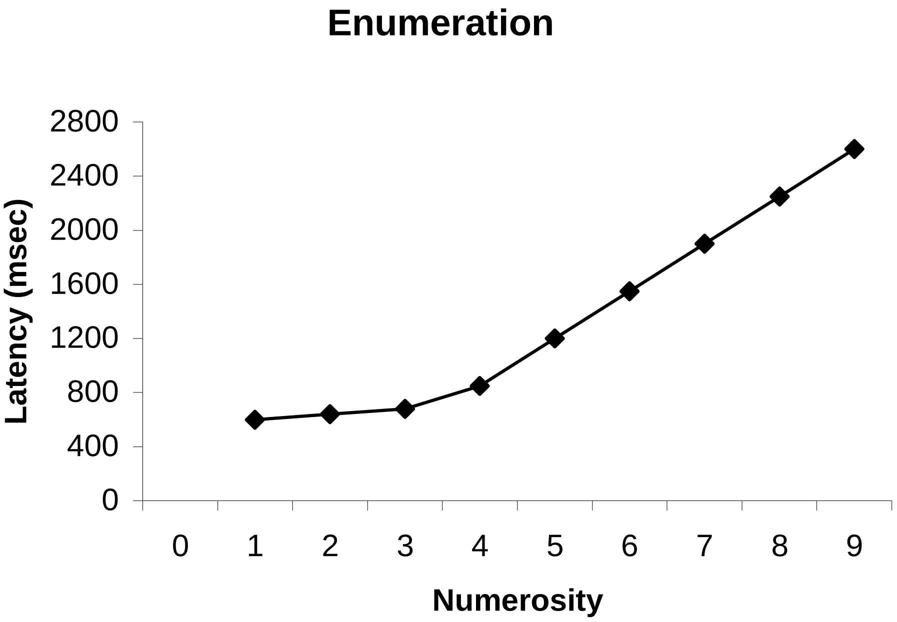


Figure 1. Example of a typical enumeration RT function.

Counting is a complex action that involves a number of stages of processing, such as individuating and localizing the items, switching attention from item to item, summing the number of items, maintaining a running total of the items and inhibiting the ‘re-counting’ of already counted items (inhibition of return) (Tuholski, Engle, & Baylis, 2001). One fundamental question is whether subitizing is qualitatively different from this, or whether the same processes are involved in both functions. The question of distinct processes has a long history in experimental psychology and still remains controversial.

Subitizing is found in all known human cultures (Butterworth, 1999), across wide age ranges (including infants: e.g. Antell & Keating, 1983) and even in non-human animals (e.g. Hauser, MacNeilage, & Ware, 1996). Counting, in contrast relies on language and is therefore hypothesised to be culture-bound (Butterworth, 1999).

Some researchers strongly deny the existence of a significant change in behaviour and suggest a single process underlies visual enumeration (Vanoeffelen & Vos, 1982; Balakrishnan & Ashby, 1991; 1992). They argue that the time to enumerate is a non-linear function of the items present. Others (e.g. Gelman & Gallistel, 1978) accept the behavioural discontinuity, but seek to explain enumeration as a purely serial process which acts at different rates for different target sizes. For them, subitization is just fast serial counting. Subitization is fast because it is non-verbal and counting is slower because it has an added verbal counting load.

Even amongst those who argue that subitization depends on special-purpose operations, there is disagreement about the nature of the critical visual process. One account proposes that subitizing depends on the recognition of a small number of distinguishable patterns (Mandler & Shebo, 1982). According to these authors larger numbers cannot be enumerated by this pattern recognition process because the patterns formed by larger numbers are both more variable across instances of the same number and more similar across instances of different numbers. Support for this latter view has also come from findings where familiar patterns of larger numerosities yielded “subitizing-like” behaviour with fast slopes (Mandler & Shebo, 1982; Wolters, Vankempen, & Wijlhuizen, 1987; Lassaline & Logan, 1993; Palmeri, 1997). In addition, Logan & Zrobodoff (2003) demonstrated that participants rate different patterns of the same numerosity as more similar within the subitizing range than outside the subitizing range, in favour of a pattern-matching account for subitizing.

A third hypothesis argues that subitizing is reliant on a parallel preattentive process which is distinct from pattern recognition but also from the serial process of counting (Julesz, 1984). According to this account subitizing rests on a distinct set of visual processes that can be distinguished from processes involved in counting. For example, Trick and Pylyshyn (1993; 1994) propose that subitizing is dependent on the parallel application of a limited set of special purpose visual processes, which they term FINSTs (Fingers of Instantiation), which index a small number of visual locations. The same underlying system is used for tracking sets of objects (Pylyshyn, 1989). Due to the limited set of FINSTs, larger numbers of stimuli require a separate counting process.

In a more general number apprehension theory, Feigenson, Dehaene and Spelke (2004) also suggest two separate core systems of number: one system for representing large, approximate numerical magnitudes, and a second system for the precise representation of small numbers of items. The approximate system is deemed to be sensitive to the ratio between numerosities, whereas the exact system responds to the absolute number of individual items, with a limit of about 3. The system representing exact small numbers may be served by the special purpose subitization process (parallel processing of elements and/or pattern recognition). The approximate number system, however, is distinct from counting, where exact numbers must again be represented.

Neuropsychological evidence

One way to distinguish between distinct brain processes is to assess whether there are neuropsychological deficits associated with damage to one but not the other process. However, while there have been numerous case reports of enumeration difficulties in brain-lesioned patients (e.g. Holmes, 1918; Mcfie, Piercy, & Zangwill, 1950; Warrington & James, 1967; Seron et al., 1991; Cipolotti, Butterworth, & Denes, 1991) there has been surprisingly little neuropsychological research published on explicit distinctions between subitizing and counting.

Cipolotti et al. (1991) reported a single case study on a dyscalculic patient C.G., who suffered from damage to the left fronto-parietal region. Primary dyscalculia has been defined as an impairment in number processing and number knowledge that cannot be accounted for by difficulties in other faculties such as memory and language (Berger, 1926). Acalculia is often observed together with finger agnosia, agraphia and left-right disorientation, these symptoms are collectively called Gerstmann’s syndrome (Gerstmann, 1940), although they can be dissociated from each other (Benton, 1977). C.G. demonstrated the classical signs of Gerstmann’s syndrome, but strikingly had a preserved ability to deal with numbers below 4, while she was completely impaired at dealing with any larger numbers. She could not count beyond 4, read numbers beyond 4 or do any calculations beyond 4. She could however enumerate up to four items, but did this through serial counting rather than subitizing. Dehaene and Cohen (1994) required 5 simultanagnosic patients to enumerate displays of 1-6 items. All 5 demonstrated accurate performance on smaller numerosities (up to 3), while their counting of larger numbers was severely impaired. Dehaene and Cohen proposed that the patients had a problem in keeping track of previously visited spatial locations. However, the study failed to specify whether this was specifically a problem related to visual memory or whether other aspects of counting were impaired (e.g., keeping a running track of items in verbal memory). In addition it was not clear whether despite good accuracy, their subitizing speed was impaired or not. Also, it may still be the case that performance in the counting range puts particular stress on processes such as keeping a running index of items, so that the dissociation between apparent subitization and counting may reflect a quantitative deficit in a more difficult process rather than a qualitative shift in visual processing mechanisms.

Other authors have described patients who, despite good accuracy rates, present with impaired subitizing speeds. Lemer et al. (2003) reported patient LEC who had a focal lesion of the left parietal lobe, Gerstmann’s syndrome, and simultanagnosia. LEC presented with a deficiency in subitizing as measured through enumeration times, despite good accuracy. Similar results were found by Ashkenazi et al. (2008) with patient AD, who presented with a left IPS lesion. Similarly again, Halpern et al. (2007) demonstrated impaired subitizing speed in 16 patients diagnosed with corticobasal degeneration (CBD) (although their accuracy was almost at ceiling). In a task where participants had to match dot displays to Arabic numerals, the CBD group demonstrated significantly larger RTs than a group of patients with frontotemporal dementia as well as a group of healthy age-matched controls, for numerosities lower than 4. Importantly, the CBD patients also required increasingly longer latencies to judge greater magnitudes in this subitizing range. This suggests the CBD patients adopted a ‘counting’ strategy in the subitizing range. Again, their counting RTs for larger numbers were also impaired. An argument against dissociative processes can also be mounted from the neuropsychological literature. In some patients with bilateral parietal lesions and Balint’s syndrome (Balint, 1909) enumeration of even one or two elements can be error prone (e.g. Humphreys, 1998). In all of the above cases it remains possible to argue for a deficit in a single counting process, which simply becomes more difficult at larger display magnitudes. In summary, the neuropsychological evidence to date also does not unequivocally support a 2 process account. One of the main questions that is addressed in this thesis is whether subitizing truly is special and can be dissociated from counting, following brain lesion. In this thesis I will present a single case study of a patient who presented with normal subitizing along with impaired counting (Chapter 3), suggesting that at least some processes are specific to counting and are not required for subitization and supporting at least 1 version of the 2-process account. I will expand on this further in the aims and overview of the thesis.

Functional Imaging evidence

Findings from neuroimaging studies with healthy participants also provide inconclusive evidence as to whether enumerating small number is based on a dissociable process from enumerating large numbers.

To date, very few imaging studies have directly compared subitizing and counting. Sathian and colleagues (1999) conducted a PET study in which observers had to enumerate the number of vertical bars in a grid that always contained 16 bars (enumeration amongst distractors). They compared counting relative to subitizing of targets that popped out from distractors, as well as detecting single targets. They found that subitizing was associated with activation of bilateral occipital extrastriate cortex, most notably the right middle occipital gyrus, when compared with detecting a single target. Activations associated with counting larger numbers, compared with subitizing, involved the same areas as above (bilateral occipital extrastriate cortex) as well as additional parietal and frontal regions (bilateral superior parietal lobe/intraparietal sulcus, right inferior frontal regions, and anterior cingulate).

Subsequently, Piazza et al. (Piazza, Mechelli, Butterworth, & Price, 2002) again used PET to measure brain activity when counting dot patterns. They also found no separate regions to be more active for enumerating small numbers compared to larger numbers. For the opposite contrast (counting more active than subitizing), they found enhanced activation in bilateral middle/inferior occipital extrastriate cortex as well as in the left posterior intraparietal sulcus and right cerebellum. Because they found no separate neural system for enumerating small numbers that was not involved in the counting of large numbers, they suggest that subitizing and counting are not implemented as functionally separate processes.

In a similar experiment, this time with fMRI, Piazza and colleagues (2003) found no greater activation for subtizing than counting anywhere, along with a large network of occipital (calcarine, middle occipital), parietal (anterior and posterior IPS), insular, prefrontal and subcortical areas that were more activated for counting than subitizing. However they also demonstrated that, while for a large subset of these counting specific regions, the activation increased linearly as the number of items increased from four to six items, there was no region showing increasing activation from one to three elements. This last result is consistent with subitizing operating on the basis of parallel visual processes, and counting on serial processing.

These increased activations associated with counting, compared with subitizing, are perhaps not surprising given that counting involves more mental processes than subitizing (individuating and localizing the items, switching attention from item to item, summing the number of items, maintaining a running total of the items and inhibiting the ‘re-counting’ of already counted items (Laeng, Kosslyn, Caviness, & Bates, 1999; Klein, 2000; Tuholski et al., 2001). In this light, rather than comparing subitizing with counting, a more indirect way of assessing subitizing was proposed by Ansari et al. (2007), who used dot patterns in a number comparison task, where 2 patterns were presented sequentially. Participants pressed one button if the first array was numerically larger, and another if the second display was numerically larger. This allowed them to assess whether numerosities in the subitizing range were processed differently from larger numerosities that may be counted or (in this task) estimated. They found greater activation for small compared with larger number comparisons in the right temporo-parietal junction and greater activation for large>small in the calcarine sulcus and the parieto-occipital sulcus. In addition, activation in the TPJ was suppressed relative to baseline in the large numerosity condition. The authors explain these results in terms of the stimulus-driven “bottom-up” attention being linked to subitizing and goal driven, “top-down” attention being linked to larger number processing. The apparent inhibition of the right TPJ is consistent with this top-down argument, since other work shows that there is inhibition of the right TPJ under conditions where participants must monitor a stream of distracter objects for a target, TPJ deactivates until the target is detected (Shulman, Astafiev, Mcavoy, Davossa, & Corbetta, 2007). Conjunction analyses for small and large number processing did strongly implicate bilateral regions of the IPS, for both symbolic and non-symbolic numbers, strengthening the idea that the observed differences in the TPJ were likely to be related to attentional differences, rather than number-specific processes.

Hyde and Spelke (2009) also compared the processing of small quantities of dots (1-3) to larger numerical quantities (8-24) outside of an enumeration paradigm, by measuring event-related potentials to the same or a different number of dots in a passive viewing adaptation paradigm. They found that an early-evoked component (N1), observed over widespread posterior scalp locations, was modulated by absolute number with small, but not large, number arrays. In contrast, a later component (P2p), observed over the same scalp locations, was modulated by the ratio difference between arrays for large, but not small, numbers. This fits with Feigenson et al.'s proposal of two separate core systems of number (Feigenson, Dehaene, & Spelke, 2004).

Attentional Mechanisms

The ability to subitize visual information may link to our ability to integrate information from complex visual environments in order to perceive a coherent representation of the visual world. One traditional view of this ability, exemplified in the Feature Integration Theory (Treisman, 1998), is that our perception of a coherent environment is generated from serial 'fixations' of attention, which are necessary in order to bind information at the attended locations. While the individual features of objects can be processed in parallel, more complex representations, based on the relations between these features, are thought to require serial attention. Although much work supports this view, particularly from search experiments where multi-featured targets must be discriminated from distractors (Treisman & Gelade, 1980; Wolfe, 1998), other work suggests that relatively complex information can be derived in a spatially parallel manner. For example, participants can rapidly derive information about the gist of a scene (Biederman, 1972; Thorpe, Fize, & Marlot, 1996; Torralba, Oliva, Castelhano, & Henderson, 2006), consistent with gist being realised from spatially parallel processes. This may be the process of subitization. Indeed, patients who are impaired at subitization are typically highly impaired at identifying scenes (e.g. Humphreys, 1998) – as is found in clinical cases of Balint's syndrome.

Treisman (2006) has recently argued that there may be two modes of attending to scenes, focused and distributed attention, brought about by evidence indicating that properties of scenes can be extracted in parallel when a distributed mode of attention is adopted. This is illustrated by work on visual averaging (Ariely, 2001; Parkes, Lund, Angelucci, Solomon, & Morgan, 2001; Chong & Treisman, 2003). Chong and Treisman (2005), for example, found that extracting the mean from a set of items was easier to combine with tasks requiring distributed attention than with tasks requiring focused attention. They propose that statistical properties are automatically available when one distributes attention across the visual scene. According to this work, distributed attention provides information about the statistical properties of scenes at a glance, but it may not provide precise information about the individual stimuli present – for which focused attention is needed. One question which arises, then, is how these two modes of attention relate to one another. Is a distributed mode of attention related to subitizing or estimating (or both processes)? This was examined here by assessing whether patients with Balint's syndrome could adopt a distributed mode of attention, and demonstrate a relatively preserved estimation performance, despite subitization itself remaining highly impaired. Estimation may depend on distributed attention but subitization itself may be independent of attention. Consistent with this, patients with a chronic attentional bias to one side of space (e.g., in the syndrome of 'visual extinction'), who fail to report items in the contra-lesional field, can nevertheless enumerate up to four items when two of them are in the neglected field (Vuilleumier & Rafal, 2000). This suggests that subitization may not require that patients attend to individual stimuli.

In contrast, counting may depend on a form of focused attention, in which each item is selected in turn. To be successful, such a serial attentional process would need to be supported by other processes, such as spatial indexing, switching attention from item to item and inhibition of return (Laeng et al., 1999; Klein, 2000; Tuholski et al., 2001).

Other evidence for subitization being separated from attentional demands comes from Watson and colleagues (Watson, Maylor, & Bruce, 2007). These authors demonstrated a sharp increase in saccades for enumeration of more than 4 items. In addition, when eye movements were prevented, counting became less efficient and accurate, whereas subitizing remained rapid and accurate. Simon and Vaishnavi (1996) investigated enumeration of dots in afterimages and also found that subitizing was perfect and unaffected, whereas enumeration of more than 4 objects was much more error prone.

On the other hand the idea that subitizing is truly ‘pre-attentive’ has come under fire in a recent series of studies which have shown that the enumeration of small numbers can be affected by manipulations of attentional load. For example, Vetter et al. (2008) showed effects of a dual task load on subitization, where the primary task was a speeded target detection task at the fovea which implemented the manipulation of attentional load. Under low load, subjects detected a simple feature (the colour red, independent of spatial arrangement), whereas under high load, subjects detected specific conjunctions of colour and spatial arrangement. As a secondary task, subjects judged the number of target Gabor patches ranging from 1 to 8 in a circular arrangement around the centre stimulus. Subitizing accuracy was impaired under both dual-task conditions compared to single task conditions, and was more severely impaired on the high-load task. It should be noted though that this study examined the enumeration of targets amongst distracters, and this process of distractor segmentation may itself be attentionally demanding. For example, Watson et al. (2002) found that older participants did not show evidence for subitization when distractors were present, but did when there were no distractor items (see also Watson & Humphreys, 1999 for neuropsychological evidence).

Other studies varied the attentional resources available by having participants focus attention on another stimulus prior to enumeration taking place (using so-called ‘attentional blink’ procedures (e.g. Olivers & Watson, 2008; Egeth, Leonard, & Palomares, 2008). In a rapid serial visual presentation paradigm of letters and a dot display, the studies found that only the detection of one dot was not affected from the preceding letter identification task, but the more dots there were (within the subitizing range), the more enumeration suffered. With this, they demonstrated that subitizing is susceptible to a reduction in attentional resources and hence not pre-attentive. Similarly, in an inattentional blindness paradigm, Railo and colleagues (2008) found that only numerosities of 1 and 2 could be enumerated when the effects of attention were minimized.

Subitizing may indeed not be pre-attentive and demand some attentional resources, which may be reflected in the small positive slope even in the subitizing RT function. However, it is conceivably still less attention demanding than counting, and the distinction of these two parts of the enumeration function is not dependent on subitizing being pre-attentive. Subitization may also be more automatic – in the sense that it is more difficult to shut off even if it is irrelevant or even detrimental to the task. This was examined in Chapter 5 here. This Chapter focused on the effects of repeating stimuli across trials with the same number versus the same response category (but different in number). Relative to the same number condition, there was a consistent slowing of the response to small number displays in the same-response (different numerosity) condition; this did not occur with displays with larger numbers. This is consistent with participants being unable to stop computing that consecutive displays had different (small) numerosities even when they belonged to the same response category (i.e., fitting with an argument for automatic processing of small number). With larger numbers of items, there may be computation of an approximate number representation which is the same both when items have the same and when they have different numerosities, and hence there are differential carry-over effects for small and larger numerosity displays.

Visual short term memory, individuation and identification

The subitizing limit of 4 can also be framed in object perception theories, where visual object perception is typically constrained to the 'magic number four' (Cowan, 2001). This is often thought to reflect the capacity limit of visual short term memory (VSTM) (Luck & Vogel, 1997; Zhang & Luck, 2008).

Xu and Chun (Xu & Chun, 2009)'s neural object file theory suggests two components of visual processing: object individuation and object identification. There is a first stage of forming proto-objects (influenced by grouping), followed by a stage of individuating a small number of objects (fixed capacity limit of 4), and finally these are coded into objects in VSTM. Different neural regions are shown to underly both components, with the inferior IPS responding to the number of 'individuated objects' present and the superior IPS involved in 'object identification'

Subitizing in this framework can then be thought to reflect object processing at the individuation stage, with its capacity limitation determining the subitizing capacity. This neural object file theory is somewhat reminiscent of Humphreys (Humphreys, 1998) dual coding account, only this distinguished between two parallel processes: 'within-object' and 'between-object' coding. Both proposals assume there is parallel coding of a limited set of items parsed into 'proto-objects'. Between-object coding is based on visuo-spatial discontinuities and matches the individuation process of Xu and Chun (2009). The theories disagree on whether object individuation is followed by object indentification (Xu & Chun, 2009) or whether both processes can work in parallel (Humphreys, 1998).

Number representation

General models of number processing

Though there are many cognitive models of numerical cognition (e.g. Cipolotti & Butterworth, 1995; Gallistel & Gelman, 1992; Noel & Seron, 1993; Pillon & Pesenti, 2001; Schwarz & Ischebeck, 2003), I will only briefly describe three central models that are most cited.

The first model is a cognitive model proposed by McCloskey and colleagues (Mccloskey, Caramazza, & Basili, 1985; Mccloskey, 1992). It is an abstract modular model that is composed of three distinct parts: the comprehension system, the calculation system, and the number production system. Central to the model is an abstract, internal, semantic representation of numbers. All format specific input (e.g., digit, verbal numbers, roman, etc) is translated into this abstract representation, on which all numerical operations work, the outcomes are then again translated into format-specific output. The comprehension system converts different notations of numbers into a common abstract format.

While McCloskey's model strongly posits abstract representation, Campbell and colleagues (Campbell & Clark, 1988; Campbell, 1994; Campbell & Epp, 2004) have suggested that numbers are not represented abstractly. According to their encoding complex hypothesis, separate modality-specific number codes exist. They propose that numbers activate multiple specific representations functionally integrated in an encoding complex. Therefore, number processing is mediated by modality-specific processes (e.g., visual, digit) and not by an abstract code.

The third model is the Triple-Code Model proposed by Dehaene and colleagues (Dehaene & Cohen, 1997; Cohen & Dehaene, 1995; Dehaene, Dehaene-Lambertz, & Cohen, 1998). It combines features of the abstract modular model and the encoding complex hypothesis and is currently the most accepted cognitive model. This model does not assume a single central number representation. Instead, it assumes that there are three different codes with special and distinct functions for each. The first two codes are modality- and notation-dependent: The Arabic code, a visual number form representation, which may reside bilaterally in the fusiform gyrus (Dehaene & Cohen, 1997), is responsible, for example, for multi-digit calculations. The second code is a verbal store, which is used to comprehend and produce spoken and written number names and is also a store of arithmetical facts and tables. This is assumed to lie in the left angular gyrus (Dehaene, Piazza, Pinel, & Cohen, 2003). According to this model, it is possible to produce verbal numbers from visual number (3 -> "three"), and vice versa, without going through a central semantic bottle-neck. The third code is the abstract analogue magnitude representation. Numerical comparison and number approximation, which access the numerical representation, are performed using this third code, in which the representation, as in McCloskey's model (1992), is modality and notation-independent. This component is assumed to lie bilaterally in the intraparietal sulcus (Dehaene et al., 2003). Dehaene's model also suggests that the analogue magnitude code represents number size in a logarithmically compressed form (with larger numbers harder to discriminate).

Neural number representation

Tasks involving symbolic numbers (such as mental arithmetic and number comparisons) have repeatedly indicated the involvement of bilateral IPS in number representation (for a review, see Dehaene et al., 2003). More recently, whether this representation truly is abstract has elicited a large debate (see Kadosh & Walsh, 2009 and following peer commentary). Studies, such as, for example, Cohen-Kadosh and colleagues (2007) found no differences in number adaptation whether the number was in a written format or an Arabic numeral (‘three’ or ‘3’) in the left IPS, they did in the right IPS, suggesting that the numerical representation in the right parietal lobe is notation dependent and thus includes non-abstract representations.

Given the focus of this thesis on visual enumeration and estimation, I will not go further into this debate, but rather will discuss the studies concerned with investigating the representation of non-symbolic numerosities only.

Piazza et al. (2004) first demonstrated fMRI adaptation in the IPS during passive viewing of sets of a fixed quantity of dots (16). They found there was a marked recovery of the fMRI response in bilateral intraparietal sulci when a number-deviant stimulus appeared, compared to a stimulus that differed in local shape from the habituated stimuli. Moreover, recovery of the fMRI signal was related to the distance between the number-deviant and the adapted number, the larger the difference, the larger the recovery response. Similarly, Ansari, Dhital & Siong (2006) demonstrated parametric effects of numerical distance on the IPS with non-symbolic numerosities. Cantlon et al. (2006) used a blocked adaptation design, where a stream of visual arrays was presented containing the same number of elements (either 16 or 32) and the same local shape element (circles). They assessed recovery of adaptation to a deviant stimulus, which would either have different local shapes (squares or circles), or a different number of elements (half or double the adapted number). They found that the IPS showed a greater response to number deviants than to shape deviants (cf. Piazza et al., 2004).

In contrast to the above results, Shuman & Kanwisher (2004), in a similar experiment, found no adaptation effect for passive viewing of non-symbolic quantities. They presented subjects with blocks of stimuli that were either constant or randomly varying in each of two dimensions: the number of elements and the local shape of the elements (resulting in “number different, shape different”, “number same, shape different”, “number different, shape same” and “number same, shape same” blocks). They found no significant number adaptation effects in the IPS or any other region previously implicated in number processing. In another experiment they compared a colour judgement task with a number judgement task (on the same displays) and found no activations of the number task over the colour judgements in the IPS. This implies that although the IPS may respond to number, it is not domain specific for numbers.

Piazza et al. (2007) investigated whether number adaptation in the IPS would occur, irrespective of whether the numbers were being conveyed in a symbolic (Arabic numeral) or non-symbolic (dot pattern) format. The authors had participants passively view series of dot patterns and symbolic numbers. They found adaptation in bilateral IPS when the same number (approximately), compared to different numbers, were presented, and this was independent of whether there was a change in notation (from dot pattern to symbolic and vice versa). In other words, the IPS recovered when a deviant symbolic number was presented amongst a stream of constant non-symbolic quantities, equally as when a deviant non-symbolic number was presented amongst a stream of constant symbolic quantities. This suggests that the IPS may contain representations that respond to an abstract number irrespective of how it is presented. However, it should be noted that there were only 2 categories (≈20 and ≈50) and participants were informed of the number of dots that could appear, so it is plausible that they automatically coded the non-symbolic numerosities in symbolic terms. This would then automatically give rise to adaptation to the same abstract number whether participants viewed dots or Arabic numerals.

Aim and Overview of the Thesis

In this thesis, I aim to explore the attentional mechanisms underlying enumeration and estimation, while also assessing number apprehension in estimation through a variety of methods. After dissociating attentional modes in enumeration and estimation, a large part of the focus will be on the visual enumeration of small magnitudes. The main questions here are: Is subitizing special and dissociable from counting? And if so, are different brain mechanisms necessary for subitizing and counting? Finally, I ask whether there is a different type of number representation when people estimate small (subitizable) numerosities compared to larger numerosities (that would normally require counting), when a distributed mode of attention is adopted?

In the first empirical chapter, I present an in-depth single case study of a patient with simultanagnosia, GK, as well as a behavioural experiment where the perceptual window of normal participants was artificially limited. Here, I focussed on the different attentional modes underlying estimation and enumeration. Due to his simultanagnosia, GK has a severe impairment in visual enumeration (though his counting of non-visual items was intact). We hypothesised that estimation and counting rely on different attentional processes, with Focused attention, using a narrow attentional window, being adopted for counting; and a more Distributed attention mode, covering a wider spatial area, being adopted for estimating. This first chapter examined whether it was possible that even with severely impaired counting, estimation might be spared. This would mean that an account of simultanagnosia as having an abnormally narrowed attentional window, so that only one part of space is ‘seen’ at a time (Thaiss & Debleser, 1992) is not sufficient to capture the whole issue. It may only be correct when the patient is in a focussed attention mode and not when a distributed mode of attention is adopted. To this end, I will contrast GK’s estimation with his enumeration performance and manipulate visual grouping (by proximity, colour and collinearity) to assess how the two tasks are affected. If indeed GK has access to a more distributed attentional mode, grouping should aid his estimation, but disrupt counting. In contrast, the opposite pattern should occur when items are more easily individuated, helping counting and disrupting estimation[1].

The extent of GK's perception in a distributed attentional mode was then further explored, by assessing whether he has a representation of the visual statistics of displays. This work was published as a note in *Neuropsychologia*. Although this study is relevant to the discussion of distributed attention, it did not really assess enumeration or estimation, therefore it has been added in Appendix 2.

After presenting work on how visual enumeration varies under different modes of attention, the focus of the thesis is shifted to investigate more specifically the relations between subitizing and counting. The second empirical chapter presents a single case study of a patient with a marked inability to count numerosities that fall outside the subitizing range, while the enumeration of small numbers was spared. In this chapter I investigate whether this is due to a working memory problem, a general number apprehension problem or reflects a problem specific to serial visual enumeration. Ways to improve the patient's counting performance were also assessed, by varying whether items grouped into subitizable units (either spatially defined or by colour) and by keeping a motor record. Can spared subitization processes be used to support impaired counting? A publication based on this chapter is currently in press with Neurocase and can be found in Appendix 3.

In the third empirical chapter, I move to an analysis of the neural as well as the functional differences between subitization and counting. Here I present the first large sample lesion-symptom mapping study on visual enumeration in a group of brain-lesioned patients.

---

[1] This chapter has been published in *Journal of Experimental Psychology, Human Perception and Performance* – see Appendix 1

Thirty four patients were presented with a straightforward enumeration task, where accuracy and reaction times were measured. Using an observer independent voxel-based correlational method, the association between damaged brain tissue and specific impairments in enumeration behaviour in the subitization and counting ranges were examined. Are impairments in the different ranges linked to contrasting locations of brain lesion?

In the fourth empirical chapter, the findings on subitizing small numbers are related back to the different attentional modes. In this chapter I assessed whether, when participants adopt a distributed attention mode, different processes underlie the estimation of small (subitizable) numerosities compared to larger numerosities (that would normally require counting)? Is subitizing automatic and does it lead to the computation of exact small numbers, even in an estimation task? Can this be contrasted with an approximate number representation for larger numbers?

In order to examine this, a series of behavioural serial reaction time experiments was undertaken in which participants were asked to estimate and categorize numerosity displays into “Small” or “Large”. Whilst remaining within the same response category, consecutive displays could have: the same visual pattern, a different pattern but the same number, or a different number (but still being small or large, and so demanding the same response). The different types of response repetition were manipulated in order to assess whether performance was affected by varying pattern and exact same numbers of items, within the small and large number categories. For larger numerosities, repetitions of pattern and exact same number may have relatively little effect on performance, as there would only be an approximate representation of number. In contrast, if there is automatic coding of exact small numbers, then performance may be modulated by whether the same exact number is repeated or not. Likewise, if small numbers are automatically coded as patterns, then performance may be affected by repeating a pattern compared with when the pattern is not repeated, even when displays contain the exact same numbers of items. Further experiments were included to attempt to prise apart effects of pattern and number repetition. Other control studies were designed to ensure that differential carry-over effects between small and large number displays did not reflect variations in the physical characteristics of the displays (e.g., occupied area, density and luminosity).

Following this, the final empirical chapter assessed the relations between coding small and larger numerosities under distributed attention using fMRI. This study was designed to highlight the brain regions that may be specifically sensitive to repetitions of the same small number in an estimation task. Specifically, the experiment aimed to find the neuronal correlate of the behavioural pattern found for subitizable numerosities in Chapter 5. If subitizing is a distinct process, recruiting distinct brain regions, we should see a difference in the neural areas that respond to repetition in the subitization compared to the counting range.

Overall, the data presented in this thesis provide novel contributions to the longstanding debate on whether the processes underlying subitizing and counting are different and rely on contrasting brain mechanisms. Differences between exact and approximate number coding are related, respectively, to small and large numerosities in estimation (when a distributed attentional mode). Exact and approximate number coding of larger numbers can also be distinguished and are linked to distinct attentional modes (focussed attention for the counting of exact numbers and, distributed attention for estimating and approximate number representation)[2].

---

[2] The experimental chapters of this thesis (chapters 2-6) are presented in the format of separate self-contained papers that have either been published (chapters 2 and 3) or are submitted for publication. However, to minimize repetition, I have not kept the original introductions and have reduced the introduction for each chapter so that they are topic specific – the complete published papers can be found in the appendices. Each chapter does incorporate its own discussion.

CHAPTER 2:

DISTRIBUTED AND FOCUSED ATTENTION: NEUROPSYCHOLOGICAL EVIDENCE FOR SEPARATE ATTENTIONAL MECHANISMS WHEN COUNTING AND ESTIMATING.

Synopsis

Evidence is presented for two modes of attention operating in simultanagnosia. I examined visual enumeration in patient GK, who has severe impairments in serially scanning across a scene and is unable to count the numbers of items in visual displays. However, GK's ability to judge the relative magnitude of two displays was consistently above chance, even when overall luminosity did not vary with the number of items present. In addition, several variables had a differential impact on GK's counting and magnitude estimation. Magnitude estimation but not counting was facilitated by using elements that grouped more easily and by presenting the elements in regular configurations. In contrast, counting was facilitated by placing the elements in different colours whilst magnitude estimation was disrupted. Also GK's performance on magnitude estimation tasks was disrupted by asking him to count the elements present. The data suggest that GK can process visual stimuli in either a focused or distributed attention mode. When in a focused attention mode performance is limited by poor serial scanning of attention due to an impaired explicit representation of visual space.

This chapter has been published in *Journal of Experimental Psychology: Human Perception and Performance, 33,* 1076-1088 (2007)

Introduction

Simultanagnosia and enumeration

In dorsal simultanagnosia, a disorder associated with bilateral lesions of the parietal lobes, patients show a severe impairment in counting. Dehaene and Cohen (see also Chong & Treisman, 2005) suggested that simultanagnosic patients suffer from a general deficit of serial visual exploration due to an inability to use spatial tags to refer to object locations. Counting is virtually impossible because, without spatial tagging, patients are unable to assess when a stimulus has already been counted. Despite their problem in counting, however, all five patients reported in Dehaene and Cohen (1994) showed relatively preserved quantification of sets of 1,2, or sometimes 3 items. These neuropsychological data show that subitizing can be preserved when counting is impaired.

Coslett and Saffran (1991) have suggested that the core deficit in simultanagnosia is “an impairment in the integration of object identity and spatial location information”. This would predict that differentiation of the counted items along a nonspatial dimension, for instance colour, should improve counting. This was shown in Dehaene and Cohen (1994) for only one of the five patients, whose error rate dropped significantly on sets of 3 or 4 items when the stimuli were presented in different colours.

Attentional demands

If subitization is distinct from counting, then it is likely that some of the linked attentional processes will differ too. For example, counting may depend on a form of focused attention, in which each item is selected in turn. To be successful, such a serial attentional process would need to be supported by other processes, such as spatial indexing, switching attention from item to item and inhibition of return (Laeng et al., 1999; Klein, 2000; Tuholski et al., 2001). In contrast, subitization would appear to depend on a more distributed spread of attention, so that the multiple items present are processed in parallel (Trick & Pylyshyn, 1993).

Treisman (2006) has recently argued that there may be two modes of attending to scenes, focused and distributed attention (see also Chong & Treisman, 2005). Distributed attention provides information about the statistical properties of scenes at a glance, but it may not provide precise information about the individual stimuli present – for which focused attention is needed. It may be that simultanagnosics have an extreme limit on focused attention, so that they generally only process one object at a time.

On the other hand, there are also suggestions in the literature that simultanagnosic patients can distribute their attention across a scene. For example, even though patients report seeing only one thing at a time, conjunction errors occur when there are multiple items present, suggesting that multiple features at least are still processed (Friedmanhill, Robertson, & Treisman, 1995; Humphreys, Cinel, Wolfe, Olson, & Klempen, 2000). Similarly, simultanagnosics can attend to multiple features within objects but show deficits when asked to attend to the spatial relations between separate objects (Cooper & Humphreys, 2000; Shalev & Humphreys, 2002). The problem may be not in distributing attention, then, but in serially attending to representations of separate objects in space. Since attention may only cover multiple objects in a distributed mode, the multiple features in the different objects remain available to be bound together, leading to illusory conjunctions sometimes being formed. This may normally be prevented by attending separately to objects in turn (Treisman, 1998). If this holds, then it is possible that performance in such patients may be dissociated when they are in a focused attention mode (e.g., when counting objects) relative to when they use distributed attention (e.g., when required to report about the statistics of images – such as the relative magnitudes of two displays), with performance being particularly disturbed when in a focused attention mode.

Goal of the present study

The present study set out to investigate the relations between the different modes of attention mediating visual enumeration by studying a patient with a severe simultanagnosia: GK. GK, in contrast to the patients in Dehaene and Cohen (1994) , has no adequate spatial orienting or serial search, and, in addition, even his subitization ability seems limited (Humphreys, 1998). This is not due to some general problem in counting per se, since GK can count numbers of auditory and tactile stimuli presented to him (Humphreys, 1998; see also the Case Report here). Given GK's limited subitization ability, it is a moot point whether he can use a distributed attentional mode in processing, and whether this might influence enumeration tasks.

If the core deficit in simultanagnosia is a deficit in the integration of object identity and spatial location information (Coslett & Saffran, 1991), we can predict that differentiation of the counted items along a nonspatial dimension, for instance colour, should improve counting. If such an effect is found on counting, the question is whether it would also occur for magnitude estimation, where performance may depend less on individual items being coded and more on a representation of groups of elements (e.g., a numerous vs. a less numerous group). Estimation may be more difficult when there are multiple colours present. In contrast to the effects of colour, grouping may facilitate magnitude estimation, as it may enable all the items to be coded and compared together. However, it may disrupt counting based on the individuation of items, since elements within a group may lose their individual identities (e.g.Rensink & Enns, 1995).

If there is evidence for variables having different (even opposite) effects on magnitude estimation and counting, then an argument can be raised for there being different modes of attention mediating performance – a serial, focused mode involved in counting (and disrupted in GK) and a distributed mode mediating magnitude estimation. Furthermore, given that subitization is impaired in this patient, the distributed mode of attention mediating magnitude estimation cannot be sufficient for accurate subitizing. If a form of distributed mode of attention is preserved in this patient, this would have implications for the interpretation of the processes required for subitizing.

I report a dissociation between counting and magnitude estimation, even when similar stimulus exposure durations and task demands were used for the two tasks. Subsequent studies then assessed effects of particular variables – such as using items with different colours, using displays in a familiar configuration with elements that grouped more easily – to evaluate if the variables produced independent effects under the two modes of attention (on counting and on magnitude estimation). We discuss the implications of the results for understanding the normal relations between attention and different enumeration tasks.

GK: Case report

GK was 64 years old at the time of testing. He suffered two strokes in 1986 affecting the right occipitoparietal, the right temporoparietal, and the left temporoparietal regions. GK shows symptoms characteristic of Balint's syndrome: he has psychic paralysis of fixation, and his ability to reach appropriately to visually presented items is severely impaired. Additionally, GK encounters profound difficulties when describing complex scenes containing multiple objects and, even under free vision, appears to be unable to be aware of more than one item at a time (simultanagnosia symptoms). In Humphreys, Romani, Olson, Riddoch and Duncan

(1994) GK showed nonspatial extinction when items were presented above and below fixation (see also Humphreys & Riddoch, 2003)[3]. When stimuli are presented simultaneously along the horizontal meridian, GK shows left-field extinction; this presumably reflects the relative severity of his right-, compared to his left-hemisphere lesion. Extinction decreased when the two simultaneously presented items could be grouped (Gilchrist, Humphreys, & Riddoch, 1996; Humphreys, 1998). An MRI scan is shown in Gilchrist et al. (1996).

Experiment 2.1: Basic contrast of counting and magnitude estimation, with effects of colour and configuration.

This experiment compared the performance of GK on counting and magnitude estimation tasks and manipulated the colours and the organization of the dots. Displays contained single-coloured or multi-coloured dots which were either canonically or randomly organized.

Method

All the displays were presented on a grey background on a 17 inch monitor with 800x600 pixel screen resolution. GK was positioned approximately 70 cm from the screen. One dot always comprised 0.98 degrees of visual angle across its diameter and the dots were separated from each other by 0.98 degrees (vertically and horizontally). There were numerosities of 1, 2, 3, 4, 5, 6, 8 and 10. In the canonical conditions the patterns were either horizontally or vertically oriented. Numerosities up till 5 were displayed in one row or column, larger numerosities were positioned in two rows or columns. The dots were always displayed at the center of the screen. For the larger numerosities, there was a 0.5 degree separation between

---

[3] In this study, there was no spatial bias to report one of two stimuli in either the upper or lower visual field, rather there was bias to select just the better (and to extinguish the worse) of two stimuli. This in itself suggests that GK could operate with a spatial window of attention covering more than one shape, but then was impaired at selecting more than one shape within a normal time.

the rows/columns. In the random condition the dots were positioned randomly within the display, with a minimum distance of 1.96 degrees visual angle between any two dots.

In the single-coloured condition the dots were all black, whereas in the multi-coloured condition, no two dots were in the same colour. The colours were distributed randomly over the displays, so there was no bias towards certain colours only appearing in larger numerosity displays (for an example of the stimuli, see Figure 2). We used 10 different colours (green - RGB: 0,255,0; lilac – RGB: 255,0,255; yellow – RGB: 255,255,0; pale blue – RGB: 0,153,255; red - RGB:255,0,0; dark blue – RGB: 0,0,255; brown – RGB: 102, 50, 0; black – RGB:0,0,0; purple – RGB: 128,0,128 and orange – RGB: 255,153,0). The background was grey (RGB: 127,127,127) in all experiments.

For the counting experiments, the displays were presented on Powerpoint slides. The experimental procedure does not require precise timing as GK is very slow, and requires substantial presentation durations in order to enumerate stimuli. The displays were balanced over the test, so that there was an equal number of each numerosity present, and there were as many horizontally oriented as vertically oriented displays (in the canonical conditions). Before every trial, there was a fixation screen with a black cross in the centre. The fixation cross was presented for a duration of 1000 ms, the display of dots that followed was presented for an unlimited time, until a response was made.

GK was instructed to count the number of dots present in the display. All experiments consisted of 12 sessions, and in total there were 15 observations for each display. The order in which the displays were presented was randomised. The response times were measured by the use of a stopwatch and both the reaction times and the responses were noted.

In the magnitude estimation experiments, GK was shown two consecutive displays. His task was to compare the two displays and to respond which one of them had more elements in it, the first, or the second. The larger numerosity was always double the amount of dots in the smaller numerosity. The large numerosities consisted of 2, 4, 6, 8 or 10 dots. We used the same stimuli displays as for the counting tasks. The displays were balanced over the test, so that an equal number of each numerosity was presented, there were equal numbers of horizontally oriented and vertically oriented displays (in the canonical conditions), and the order of the two consecutive displays was balanced. Each trial consisted of a 1000 ms presentation of a fixation cross, followed by two consecutive display presentations for 3000 ms each. Under these conditions, no apparent motion was present, when one display changed to the next. The data were gathered in 20 sessions, resulting in 40 trials for every condition.

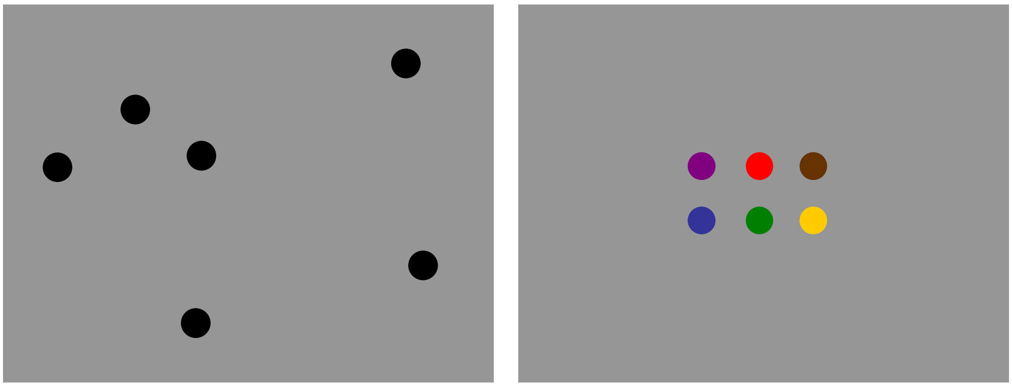
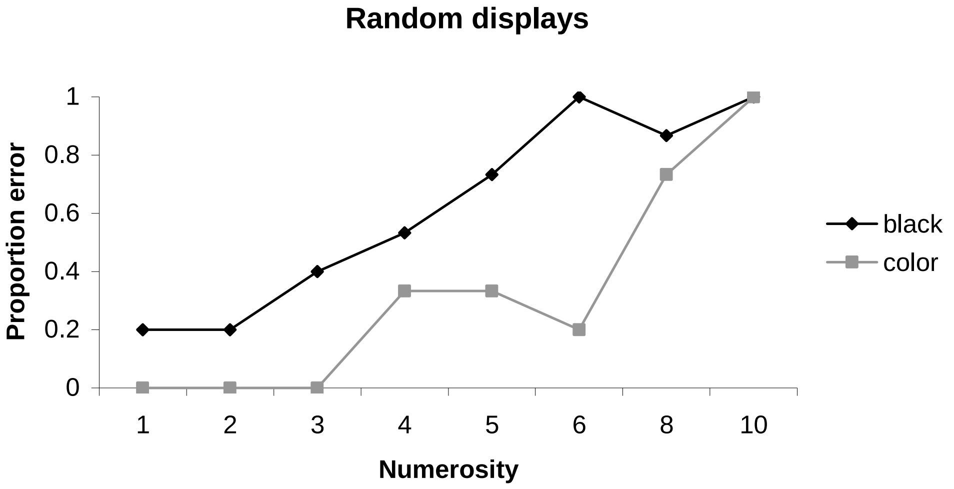


Figure 2. Example displays from Experiment 2.1. Left: random, black dots; right: canonical, multi-coloured dots.

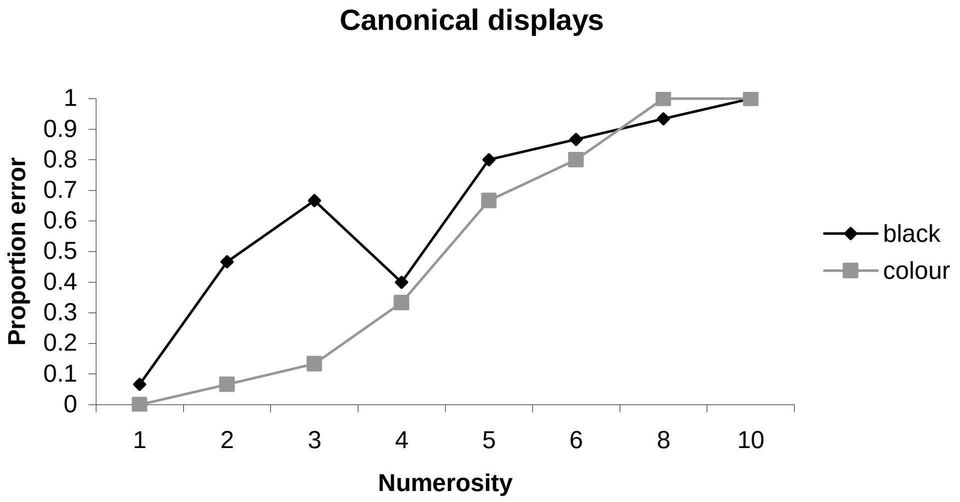
Results

<u>Counting.</u>

In the single-coloured condition, GK showed a severe impairment in counting the dots, both in canonical and in random displays (Figure 3). The error rates showed a linear increase from small to large displays. A linear regression analysis (for the single-coloured dots) indicated that 71.4 percent of the variation in errors can be predicted from the presented numerosity. The linear relationship between these variables was highly significant (F(1,238)= 596.78, p< .001). Remarkably GK did not report all the 1 dot displays correctly, and he made mistakes for all numerosities. There was no evidence for preserved subitizing. The rise in performance for numerosity ‘4’ in the canonical condition could partly be explained by guessing: when we regard the overall prevalence of answers, GK responded ‘4’ on 38 occasions, while each display was only shown 15 times. Average reaction times of the correct responses for each condition separately as well as an overall average are presented in Figure 4. These showed a significant linear relationship with the presented numerosities (F(1,209)=111.49, p< .001), with 34.8 percent of the variation in the average response time accounted for by the variation in the presented numerosities (departures from linearity occurred only at the largest display sizes too, and there was no evidence for departures from linearity around the normal numbers for subitization). The reaction times are consistent with a serial counting process, and there was no evidence for a fast parallel processing of the smaller numerosities.



(a)



(b)

Figure 3. The proportion of errors made by GK when counting in Experiment 2.1. (a) Random displays; (b) Canonical displays.

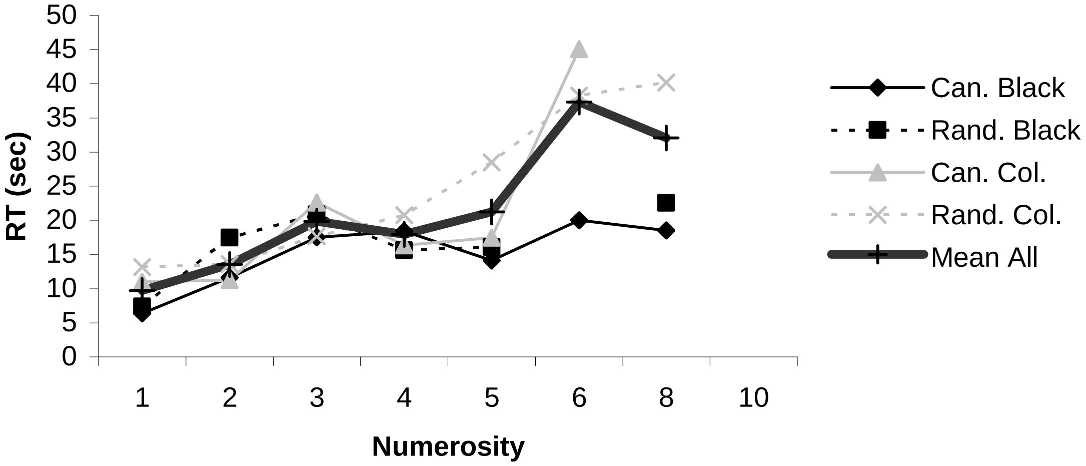


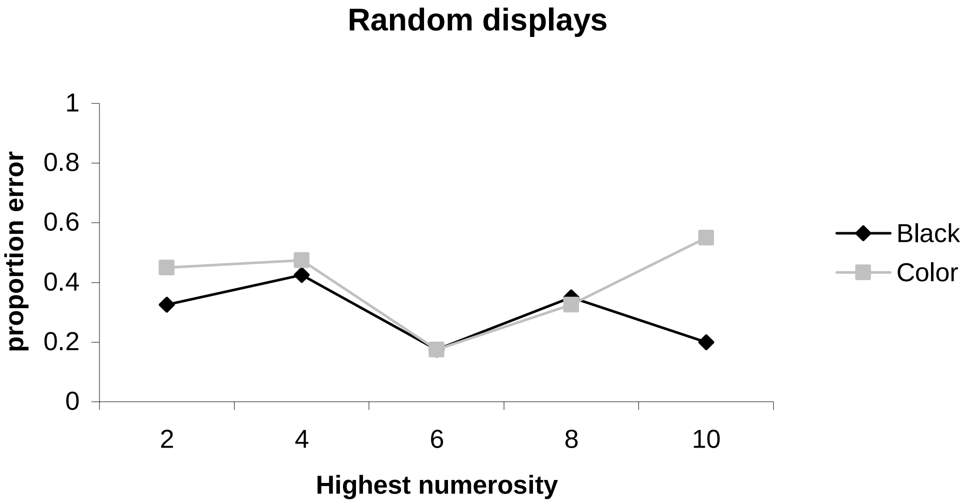
Figure 4. RTs (sec) for correct responses in all 4 conditions (black and multi-coloured items, in random or canonical positions), plus the average RT over the 4 conditions

The data in all conditions showed a significant effect of numerosity (overall χ^2 (1)= 149.8, p< .001). This shows that although GK made errors on the low numerosities, they were still ‘easier’ than the higher numerosities (76.3 % correct for displays 1-4 vs. 20.4 % for displays 5-10). GK found it increasingly difficult to keep track of the number of items as the numerosity increased. Also, there was a significant overall effect of colour (χ^2 (1)= 27.113, p< .001; 36.7 % correct for single colour displays vs. 60 % for multi-colour displays). GK's performance in the single-coloured dots condition differed significantly from the multi-coloured dots condition, both in canonically organised displays (χ^2 (1)= 7.467, p= .006) and in randomly organised displays (χ^2 (1)= 21.654, p< .001). The colour manipulation reliably improved counting (Figure 3 a & b). Finally, GK's performance in counting multi-coloured dots was improved by a random distribution of the dots across the display, compared to the canonically organised displays (χ^2 (1)= 5.625, p=0.018). There was no improvement in counting randomly - as opposed to canonically - organised single-colour displays (χ^2 (1)= 0.162, p=0.687). This might be because GKs ability to count single-coloured items was at floor level.

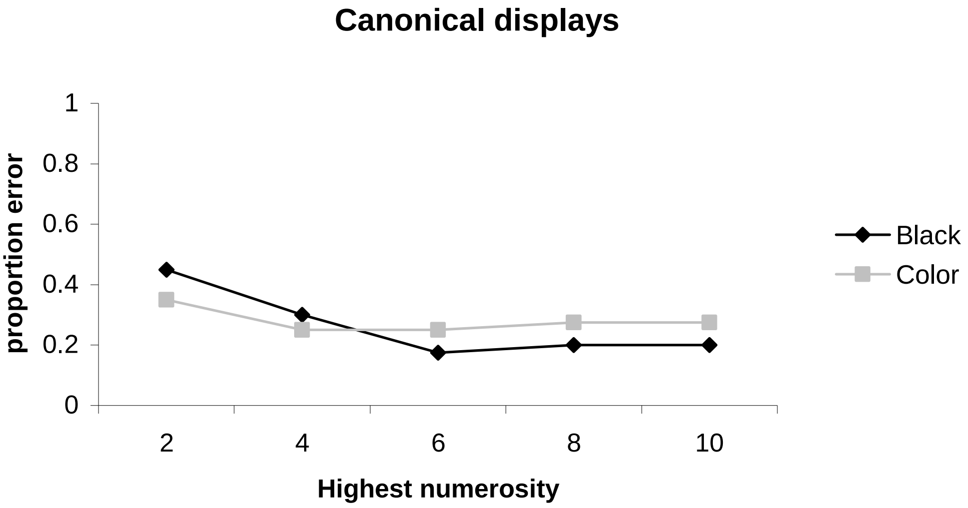
In order to assess the types of errors, GK's responses were first correlated with the presented numbers. This resulted in significant correlations for the multi-coloured displays in both canonical (r =0.858, p<.01) and random (r= 0.956, p<.01) displays. The single coloured displays also showed significant correlations between the presented numbers and the responses, again in both canonical (r= 0.669, p<.01) and random (r=0.660, p<.01) organisations. Next the range of errors was evaluated. In order to assess whether there were more 'close' errors (defined as responses that differed by 1 or 2 from the actual number presented) than 'far' errors (responses that differed by more than 2), I compared the frequencies of these ranges of errors for each condition separately. There were no significant differences in the number of close to far errors in the single coloured condition, both for the canonical (χ^2 (1)= 2.105; p= .147) and the random displays (χ^2 (1)= 1.952; p=0.162). For the multi-coloured displays, there again was no significant difference in the range of errors in the canonical condition (χ^2(1)= 1.071; p=.301), but there were significantly more 'close' than 'far' errors in the random condition (χ^2(1)= 12.512; p<.001).

Estimating

For both the canonical and the random displays, GK's performance was significantly above chance (Figure 5), over all numerosities (black canonical: χ^2(1) = 23.38, p< .001; multi-coloured canonical: χ^2(1) = 20.35, p< .001; black random : χ^2(1) = 17.55, p< .001; multi-coloured random: χ^2(1) = 4.46, p= 0.035), showing that he was able to compare numerosities.



(a)



(b)

Figure 5. Proportion of errors in the estimation task in Experiment 2.1. (a) Random displays; (b) Canonical displays.

There was an overall effect of numerosity size (χ^2(1)= 4.723, p= 0.030). GK made fewer errors when comparing the larger displays as opposed to the smaller displays (62.2 % correct for trials with largest numerosities 2&4 vs. 70.3 % for largest numerosities 8&10). When the data were divided, there was a marginally significant difference in accuracy between larger and smaller numerosities for canonical displays (χ^2(1)= 3.905, p= 0.048), but no difference for randomly organized displays (χ^2(1)= 1.317, p= 0.251). Overall, GK was also significantly better at comparing canonical than random displays (χ^2(1)= 4.926, p= 0.026). Although there was no overall effect of the colour manipulation (χ^2(1)= 3.098, p= 0.078), for the random displays only, GK made significantly fewer errors with single-, compared to multi-colour displays (χ^2(1)= 4.425, p= 0.035).

Discussion

The results from the counting task showed that GK was extremely poor at counting and that although his accuracy for the smaller numerosities was relatively good, his reaction times demonstrated serial counting even for these smaller numerosities, therefore showing no sign of classical subitizing. This replicates prior data (Humphreys, 1998). Although a significant linear fit was made to the errordata, his performance on enumerating small numerosities, especially when the items were multi-coloured, was better than for larger numerosities. However, rather than this demonstrating preserved subitizing, the advantage for counting multi-coloured is consistent with GK having impaired location codes. Therefore, when the items could be individuated on another basis than location, his enumeration of up to 3 items was perfect, the errors from numerosity 4 onwards are likely to reflect working memory demands (remembering which colours had already been counted), rather than a difference between preserved subitizing and impaired counting. There was a reliable effect of whether the items were spatially random or in a familiar configuration and his counting of displays with multi-coloured tokens was better than his counting of black items. Indeed, with multi-coloured dots, GK's counting of random displays was better than his counting of configural displays, particularly for the larger numerosities. This may be because the spacing between the items was on average larger in the random relative to the configural stimuli. It is possible that, with small spacing, some colours merged as a function of GK's poor location coding (Humphreys et al., 2000), so that the counting of multiple colours was disrupted. The advantage for counting multi-coloured over black items is consistent with GK having impaired location codes, that ought to support the indexing and serial scanning of attention, and it matches prior data from patients with parietal lesions (Dehaene & Cohen, 1994). The fact that GK could not count as few as 3 items without making 40 percent errors also indicates the severity of his problems with spatial indexing, if indexing processes are important for subitization (cf. Trick & Pylyshyn, 1994).

Although GK's counting of visual stimuli was poor, he was above chance at the estimating task, over all numerosities. His performance did improve at the larger numerosities, which might be because the magnitude of the differences between the comparison patterns then increased. It might be argued that the above chance performance on the estimation task was because there were large disparities between the stimuli that had to be compared. Note, however, that GK's errors on counting were often considerably different from the number of items presented, and on 42 percent of the trials his counting responses were wrong by a factor of two or more. Thus, the above chance performance on estimating was unlikely to be due to the magnitudes of the differences used. In this respect, it is interesting to note that GK was better at estimating with configural than with random displays, which is the opposite of the pattern we observed with counting. In addition, GK showed an advantage for estimating black dots compared to multi-coloured dots – which again dissociates from the data on counting. These qualitatively different patterns of performance suggest that contrasting information may contribute to GK's counting and estimating performance. With counting, factors that individuate items (multiple colours, on average wider spacing) facilitate performance. With estimating, factors that contribute to grouping the elements (same colours, smaller spacing and/or regular configuration) may benefit performance. This would be consistent with GK being able to encode groups of items, but primarily when he adopts a distributed mode of attention in order to estimate the number of items present. This argument was confirmed in an experiment comparing performance with single coloured collinear squares to dots in canonical organisations. Although there was no difference in accuracy when counting canonically organized squares (50/120 correct) versus dots (42/120 correct - $\chi^2(1)= 1.12$, p=.28); estimating was significantly better for the displays containing collinear squares (174/200 correct) than canonical dots (147/200 correct - $\chi^2(1)= 11.499$, p<.001). This shows converging evidence for the importance of grouping when estimating.

Overall this pattern of dissociation is consistent with there being two modes of attention: focused and distributed attention. Focused attention is used by GK in counting. In this mode of attention, performance is helped by individuating the items (assigning one colour to each item, using random rather than grouped displays). In contrast, distributed attention is used in estimating, perhaps because statistical information can be inferred (Chong & Treisman, 2005) when displays are grouped under distributed attention conditions. Under distributed attention conditions, the statistical information available from displays may be stronger when elements group than when they do not group.

Experiment 2.2: The effect of short display durations on counting.

One difference between the counting and estimating tasks in Experiment 2.1 was that (relatively) short durations were used for estimating whilst unlimited durations were used for counting. It may be that GK can derive relatively global representations of displays under short duration conditions (making him sensitive to grouping by proximity/configuration and common colour), but that this information is lost when he starts to scan attention (e.g. for counting). To test this, in Experiment 2, I had GK count stimuli that were presented for the same duration as the displays in the estimating task in Experiment 2.1, namely 3 seconds.

Method

The method was the same as that for the counting task in Experiment 1, except that the displays were presented for a fixed interval of 3 s. There were 15 trials per numerosity. Only displays with black dots were used, in both canonical and random organizations.

Results

The accuracy when counting under these short presentations was not significantly different from a chance performance (1 in 8) for both canonical ($\chi^2(1)= 1.566,\ p= 0.211$) and random ($\chi^2(1)= 2.480,\ p= 0.115$) organizations (Figure 6). It was significantly lower than when there was an unlimited amount of time available both for canonical and random displays ($\chi^2(1)= 8.52,\ p= .0035$ and $\chi^2(1)= 9.76,\ p= .0018$ respectively). Performance was poor across all numerosities, and unlike Experiment 2.1, it made no difference whether the configuration was random or a canonical pattern.

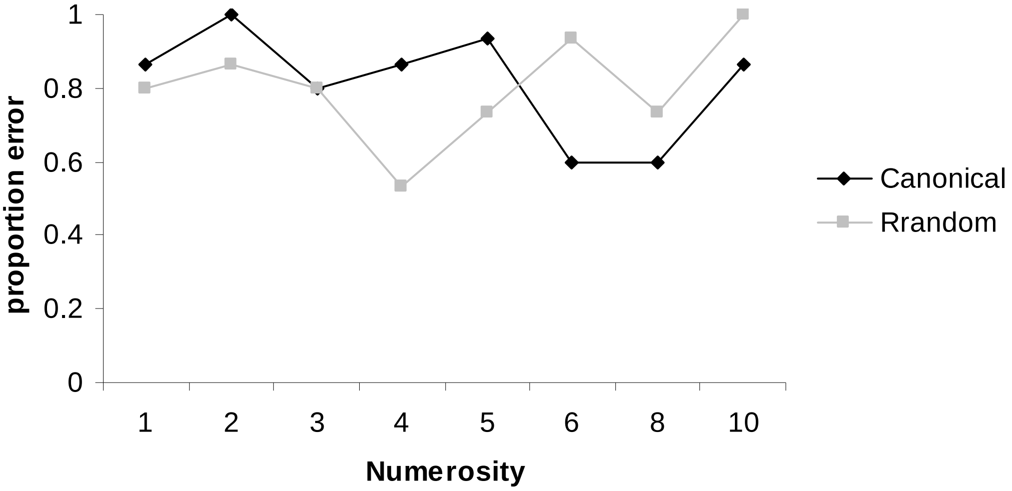
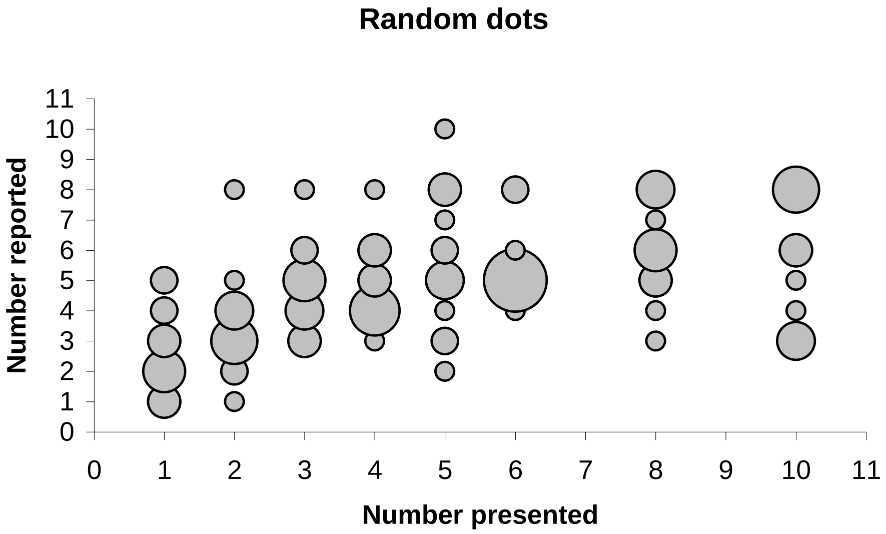
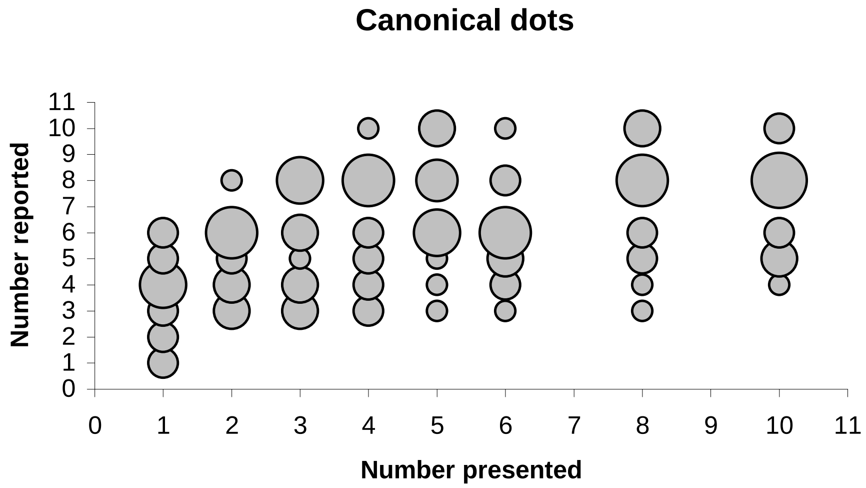


Figure 6. Proportion of errors in the counting task in Experiment 2.2.

In addition, when analyzing the responses (see Figure 7**Error! Reference source not found.**), 50.8 percent of the responses for the random displays were wrong by a distance of 2 or more. For the canonical displays this percentage was 64.2.



(a)



(b)

Figure 7. The number reported relative to the items present in Experiment 2.2. (a) Random displays; (b) Canonical displays.

Discussion

GK performed very poorly when he had to count dot displays presented for just 3 seconds and his accuracy was close to the floor. This suggests that his estimation performance is much less affected by exposure duration than his counting, consistent with him adopting different strategies. This fits with the suggestion that GK is using a distributed attention mode to respond to the statistical properties of the displays in the estimation task, and with Chong and Treisman's (2003) finding that the exposure duration of the display did not affect statistical processing. In addition, there was little evidence for a systematic relationship between the number of items and GK's response (Figure 7**Error! Reference source not found.**). Finally, there was no overall difference between counting with random and canonical figures, whereas with estimation there was an advantage for canonical displays (Experiment 2.1). However, any effect of the pattern could have been obscured by the low level of performance here. Overall, the data provide no grounds to argue that the differences between counting and estimating in the first study were due to the contrasting durations for the tasks.

Experiment 2.3: Removing effects of luminosity and equating for chance

In Experiment 2.3, I address two issues. One is the question of luminosity. Can the contrasting results for estimating and counting be accounted for in terms of GK responding to the overall luminosity of the displays in the estimation task, whereas he attempts to individuate items when counting? Note that, in Experiment 2.1, there was a direct correlation between the number of elements present and the overall luminosity of the display. With the use of single-coloured black dots on grey backgrounds, overall luminosity diminished with the number of dots being displayed. Experiment 2.3 used displays that were made up of black and white dots, shown on a grey background. There were random proportions of black and white dots in each display, so that the overall luminosity of the display did not correlate with the number of items present. Any use of overall luminosity will not benefit performance under these conditions. Experiment 2.3 also assessed whether differences in guessing could have contributed to the contrast between counting and estimating. In Experiment 2.1, there was a 1/8 probability of responding correctly on the counting task, whereas there was a much higher 1/2 probability of a correct response in the estimation task. In this experiment I contrasted counting and estimating using a 2AFC design for both tasks.

Method

This experiment was made using E-prime 1.1. Dots of the same size as in Experiment 2.1 (0.98˚) were drawn on random locations on a grey background (RGB: 127,127,127), with the constraint of a minimum distance of one dot diameter between any two dots. A random proportion of the dot display was made up of white dots, the other dots remained black. Because the proportion was chosen randomly (from zero to the total number of dots in that display), there was no correlation between the overall luminosity of a display and the numerosity present. In the counting task, GK was instructed to count the total number of dots present, and, as soon as he knew the number, he was asked to hit the space bar, and then make a choice between two numbers which were read out loud to him. These numbers were the same as the ones used in the estimation task in Experiment 2.1 (1-2, 2-4, 3-6, 4-8, and 5-10). In the estimation task the display was presented for a fixed duration of 3 seconds and GK was asked to estimate the number of dots present and was then again given the choice between two numbers. There were 16 trials per numerosity alternative, resulting in a total of 160 trials in both the counting and the estimating task.

Results

The overall level of performance was above chance both when GK used the counting strategy (62% correct, $\chi^2(1)= 4.636$, p= 0.031) and when using an estimation strategy (77%

correct, $\chi^2(1)= 22.967$, $p< 0.01$). However, GK performed significantly better when using an estimation strategy (compared to when trying to count the number of dots present, $\chi^2(1)= 7.733$, $p< 0.01$). The data are depicted in Figure 8 as a function of the largest number given in the forced-choice decision. Because there was no relation between the overall amount of luminance in the displays and the numerosity, the difference between counting and estimating cannot be attributed to GK using a luminance-based strategy.

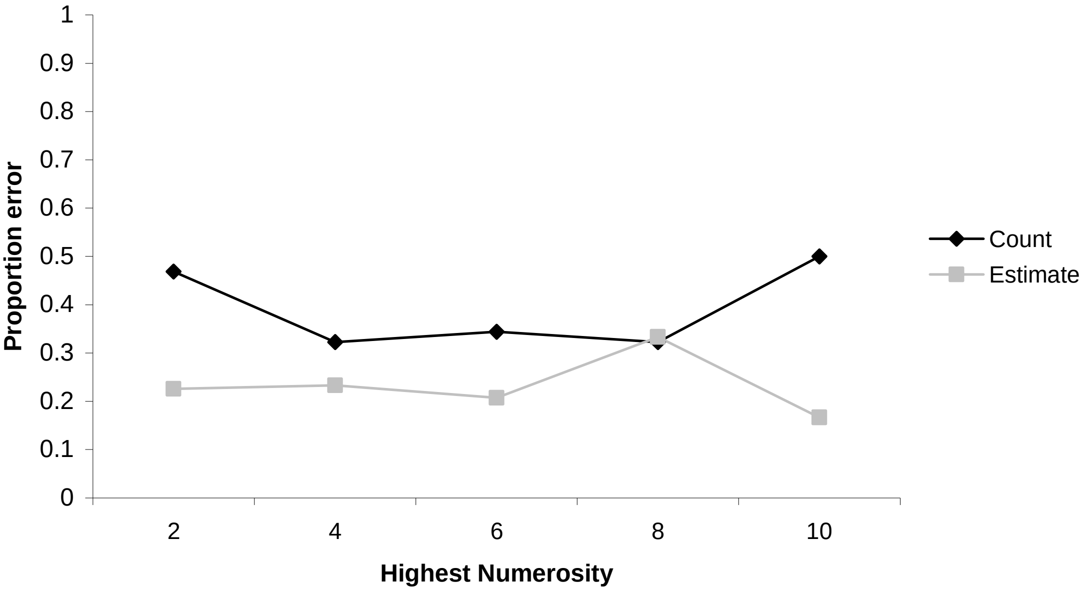


Figure 8. Proportions of errors made in the 2AFC versions of the counting and estimating tasks, performed with black and white dots. The data are shown as a function of the highest number in the forced-choice decision.

Discussion

GK was above chance at both counting and estimating, when given two-alternative forced choices to respond to, but he remained reliably better at estimating than counting. This again provides ground for the argument that GK is able to use more visual information when he estimates the number of items in a display than he can use when in a counting mode. The fact that the advantage for estimating remained here, even when I used random numbers of black and white dots also indicates that the advantage is not simply due to GK responding to the overall luminosity of the display in this condition – note that there was no relationship between luminosity and the number of items present in this experiment.

Experiment 2.4: The intentional control over attention modes.

Experiment 2.3 suggests that GK has some control over which mode of attention is adopted, since estimation remained better than counting even when similar choice responses were involved in both tasks. GK's control over his visual attention was examined further in Experiment 2.4. In this study, I asked GK to try to count the number of dots present when carrying out a magnitude estimation task.

Method

For this, I used canonical multi-coloured dot displays. I contrasted these results with when he was asked to try and look at the 'mass' in order to estimate which display had more elements (using distributed attention). There were 40 observations per pair of numerosities, in each of the two conditions.

Note that the estimation task continued to use a 2AFC procedure, with GK being asked only to vary his strategy, not to give a different answer, or guess the number of items present. Hence, if the crucial difference between GK's performance on the counting and magnitude estimations tasks was because the latter used a two-alternative forced-choice procedure (and with displays differing by an order of 2 when the numbers of items present differed), then I should again observe good (above chance) performance in estimation (though it should now be based on counting).

Results

Performance was above chance both for estimating when using a counting strategy (χ^2 (1)= 4.90, p=.027) and for estimating while trying to capture the entire display in a glance (χ^2 (1)= 20.35, p<.001). There was however a reliable difference between the two strategies (Figure 9): when using the "mass estimation" strategy, GK's accuracy was significantly higher (χ^2 (1)= 5.43, p=.019).

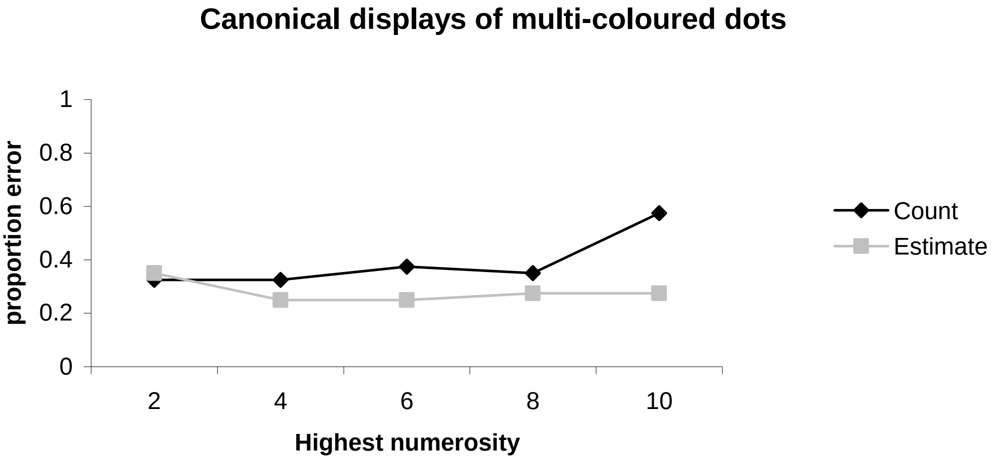


Figure 9. The proportion of errors in Experiment 2.5, when 'counting' in an estimation task. Data are shown as a function of the highest number in the forced-choice decision.

Discusssion

The results of both Experiments 2.3 and 2.4 are consistent with GK having some intentional control over his processing of visual displays, with counting being worse than estimating even with exactly the same presentation conditions. I suggest that, when asked to count the elements, GK adopts a more focused attention mode, and in this mode he is impaired at deriving statistical information from the whole display. He also has difficulty in conducting an accurate serial search of the items present; consequently his accuracy decreases. This result is also methodologically important because it indicates that the reason for GK's relatively good estimation performance was not a result of the forced-choice procedure or the display pairing used.

Experiment 2.5: Counting colours: A specific deficit in spatial tagging?

If the core deficit in counting in simultanagnosia is a problem in spatial tagging (Laeng et al., 1999), then GK may be better at counting non-spatial features than he is at counting spatial elements. For example, counting the number of different colours in a display may be somewhat easier than counting the number of exemplars of a particular colour (see Dehaene & Cohen, 1994). To investigate this, I used displays of a constant number of dots, so that there was no longer a correlation between the number of dots and the number of colours (similar to the displays used in Watson, Maylor, & Bruce, 2005). GK was asked to count the number of different colours present in the display.

Method

We created displays of 48 dots, which were positioned in the middle of a 100 x 100 pixel square cell. The screen resolution remained 800x600 and there was an imaginary grid, in which the 48 dots, with a 50 pixel diameter (0.98 visual degrees) were positioned. There were displays with 1, 2, 3, 4, 5, 6 and 8 different colours (green -RGB: 0,255,0; lilac – RGB: 255,0,255; yellow – RGB: 255,255,0; pale blue – RGB: 0,153,255; red - RGB:255,0,0; dark blue – RGB: 0,0,255; brown – RGB: 102, 50, 0 and orange – RGB: 255,153,0).The colours were randomly sampled per display. There were two configurational conditions. In the “mixed colours” condition, all colours were mixed randomly over the imaginary grid. In the “grouped colours” condition, the colours were grouped by proximity and formed clusters. In both conditions, the 48 dots were equally divided over the available colours (Figure 10). For each numerosity, there were 20 observations. GK was asked to count the number of different colours present.

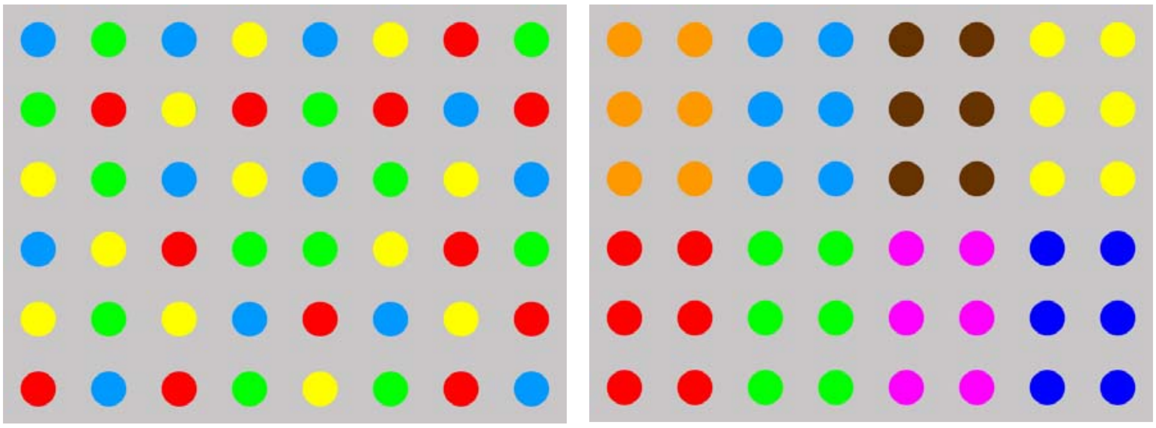


Figure 10. Example displays from Experiment 2.5 (counting colours task). Left: the "mixed colours" condition; right: the "grouped colours" condition.

Results

I investigated the effect of the spatial organisation, comparing GK's performance in the "mixed colours" condition to his performance when counting colours that formed clusters. I also compared GK's performance when counting the number of colours relative to his performance when he counted random and canonical displays of multi-coloured dots (Experiment 2.1). The results showed no significant difference between counting colours in clusters to counting randomly mixed colours ($\chi^2(1) = 1.511$, $p = 0.22$). When relating GKs performance here to the findings in Experiment 2.1, the results showed that counting the number of different colours in both the mixed and the grouped colour configurations was better than counting the number of multi-coloured shapes (Figure 11), in both canonical displays ($\chi^2(1) = 35.18$, $p < .001$ and $\chi^2(1) = 23.305$, $p < .001$ mixed and grouped respectively) and in random configurations ($\chi^2(1) = 10.14$, $p = .002$ and $\chi^2(1) = 4.063$, $p = .043$ mixed and grouped respectively). For correct reaction times, a linear regression provided a significant fit for the data (F(1,226)= 189.025, p< .001) , the variance in numerosity accounted for 45.3 percent of the variance in the response times. Any departure from linearity occurred with the highest numbers, and there was no evidence for departures from linearity around the numbers characteristic of subitization.

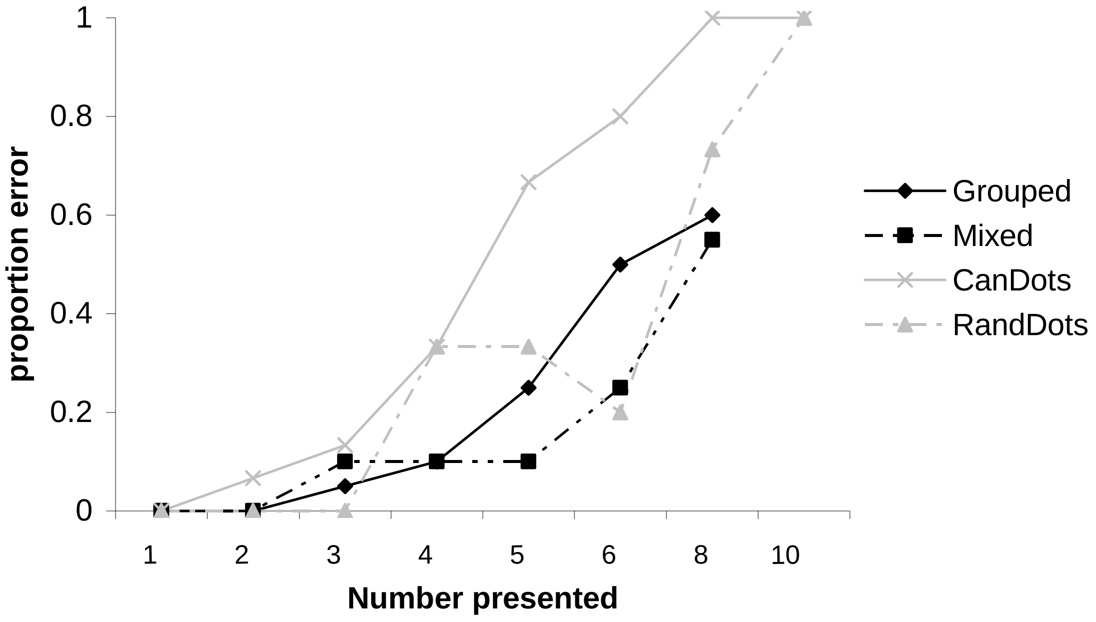


Figure 11. Proportions of errors in Experiment 2.5 for GK counting colours in mixed and in grouped displays and for counting multi-coloured dots in random and in canonical displays.

Discussion

In contrast to GK's performance when he had to count the number of coloured shapes in a display, enumeration improved when he had to count the number of different colours present. Indeed, the contrast between the experiments (counting token shapes vs counting colour features) was remarked on by GK, who noted that he 'really liked' these displays and this task. The results support those reported by Dehaene and Cohen (1994), but in an even more dramatic fashion given that GK is unable to count even small numbers of individual shapes. One reason for this contrast is that, unlike counting individual shapes, counting colours does not depend on encoding an accurate spatial representation of the stimuli (e.g., in order to prevent tokens being re-counted). Prior work has shown that GK is very poor at spatial coding, for example failing to discriminate whether shapes presented as far as 3 degrees above or below fixation fall in the upper or lower visual field (Humphreys, Romani, Olson, Riddoch, & Duncan, 1994). Moreover, GK's performance was not helped by spatially grouping the colours together in separate clusters; if anything counting mixed colours seemed to be easier. This suggests that counting colours was not necessarily based on the same information that determined estimation performance (where performance improved with grouping). The data also suggest that GK was unable to use the spatial information provided by each cluster of same-coloured items, to facilitate search. This again fits with the idea that GK is impaired at using spatial information (here even from multi-coloured displays) to guide counting. The data suggest that colour counting does not depend on accurate spatial coding, nor on gaining an overall estimation of the statistics of the visual scene; instead, colours may be counted serially within an internal 'colour space' even when location codes are damaged.

Experiment 2.6: Limiting normal vision

One account of the spatial deficit in patients with Balint's syndrome is that they are constricted in using an abnormally narrowed attentional window, so that they 'see' only one part of space at a time (Thaiss & Debleser, 1992). The data I have presented on GK's counting and estimating do not fit with this proposal, because the results on estimating suggest he can adopt a broader attentional window under some circumstances. In the final experiment presented here, I sought to provide converging evidence from normal participants that GK's performance cannot solely be explained by having a restricted attentional field. The study set out to investigate how neurologically normal participants perform on a counting task when their perceptional window is limited to (about) one object at a time. I varied whether the displays were made up of coloured or black dots, and whether the dots fell in canonical or random configurations. Do the beneficial effects of using same-colour dots and canonical configurations, which occurred for GK in an enumeration task, emerge when normal participants operate with a limited spatial window? More specifically, would the data mimic the findings with GK in a counting or an estimation mode?

Method

Stimuli

The enumeration stimuli were dot patterns on a grey background (RGB:140,140,140), with each display area being 800 pixels wide by 600 pixels high. There were between 1 and 9 dots per display. The display could be partitioned by the use of an imaginary grid with cells of 100x100 pixels. The location of each dot was always in the middle of a cell. The dots had a diameter of 50 pixels (0.98° visual angle). All stimuli were presented on a 17 inch screen with a resolution of 800 x 600 pixels and a refresh rate of 70 Hz. The experiment was programmed in Java 1.2.2 and was run on a Windows XP platform.

There were four conditions in total. Two colour conditions in which either the dots were coloured, with no two dots in the same colour (same colours as in Experiment 1, without the black), or the dots were all black. Aside from this there were also two configuration conditions, one in which the dots were displayed canonically, the other displayed dots at random positions.

In the canonical condition the dots were placed in adjoining cells, with no cell in between. In the random condition, the dots were placed in randomly sampled cells of the display. The conditions were crossed, resulting in black and multi-coloured canonical displays and black and multi-coloured random displays.

Procedure

A grey mask (slightly lighter than the background of the stimuli: RGB: 200,200,200) hid the stimulus while a square of 100x100 pixels opened randomly, showing a part of the display before the square was closed again. All 48 cells were opened at least once, so that in the end, the entire display was seen. If every cell were to be opened only once, in order to count the dots, a participant would not have to retain the location of the dot, but he or she could simply count the opened squares with dots in them. Therefore, the cells were split up in two groups, the marked cells (the cells which have a dot in them) and the unmarked cells (the cells which do not). Since the ratio of these two groups varied with the number of stimuli present (1-9 dots), I showed a fixed number of extra marked and unmarked cells. For 50% of the trials, 3 of the marked cells were shown a second time as well as 4 of the unmarked cells. In the other half of the trials, 4 of the marked and 3 of the unmarked cells were shown a second time. Because of this method, 55 windows were always opened on a trial. The timing used in this experiment approximately reflects the total duration needed by GK in order to try to count the items present.

All trials were randomised within the colour and configuration conditions. I also controlled for order effects, by mixing up the order in which participants received the four conditions.

Each trial consisted of the presentation of a focus screen for 1000ms, followed by 55 randomly opening windows showing parts of the display, each for 300ms. At the end, an answer screen was presented, where the participant filled in how many dots there were behind the mask. Each participant was given a practice session of 6 displays, so that they understood the task.

Participants

Six male controls, age-matched to GK, participated in the study, which took place across 4 sessions. The participants had an average age of 63 (56, 58, 62, 65, 68 and 69 respectively). Each participant received £18 for taking part.

Results

A repeated measures ANOVA revealed a significant effect of numerosity (F(8,40)= 44.374, p< .001, partial η^2= .899), with participants making more errors as more dots were presented. There was a reliable effect of colour (F(1,5)= 26.237, p= .004, partial η^2= .840), with multi-coloured dots yielding significantly fewer errors than single-coloured dots (see Figure 11). There was however no reliable effect of organization (random versus canonical). None of the interactions achieved significance, though there were marginal interactions between colour and number (F(8,40)=2.128, p=.055) and between colour, number and organization (F(8,40)=1.9836, p=.074).

When only the higher numerosities were considered (6, 7, 8 and 9), again a significant effect of numerosity was found (F(3,15)= 6.150, p= .006), along with a marginally significant effect of organization (F(1,5)= 4.655, p= .083), with canonical organizations yielding more errors than randomly organized displays. It is possible that the high performance in all conditions on the smaller numerosities masked this effect of canonicality in the overall analysis

I also compared GK's to this simulation of his performance with control participants. There was no reliable difference between GK's performance and that of the control group.

GK's improvement in accuracy with multi-coloured relative to black stimuli fell within 2 standard deviations of the mean improvement of the control group (mean(control)= 0.142, SD= 0.067, mean(GK)= 0.237), as did his improvement with randomly organized over canonical displays (mean(control)= 0.005, SD= 0.110, mean(GK)= 0.086).

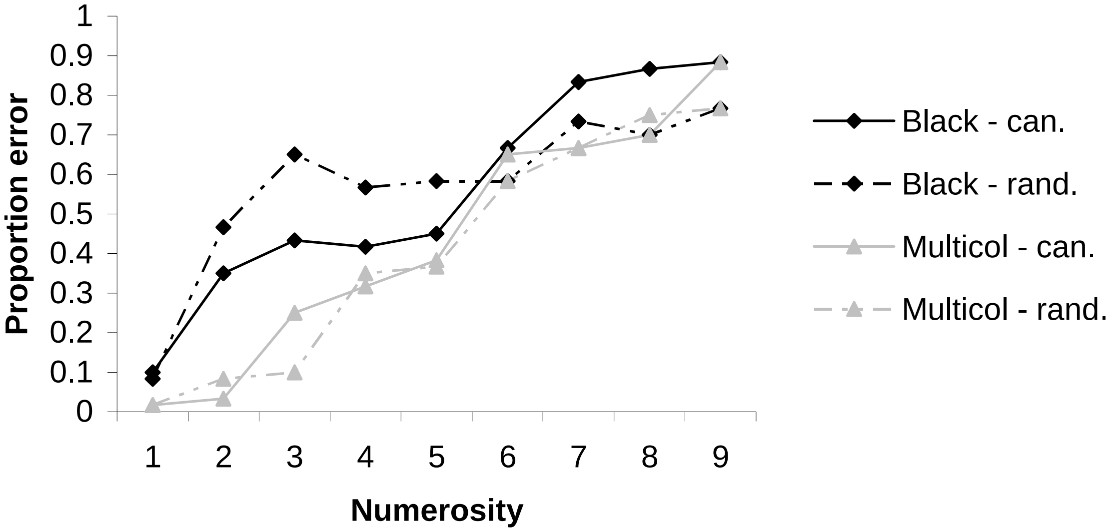


Figure 12. Proportion of errors made by control participants when counting with a limited spatial window (Experiment 2.7).

Discussion

These results largely replicated the performance of GK in the counting task. When counting, GK showed an advantage for multi-coloured over single-coloured displays and for random over canonical configurations. When controls were given a limited visual field, they, like GK, benefited from the presence of multiple colours. Although there was no general effect of configuration with the control group, there was a trend towards improvement with randomly organized displays compared to canonical displays when performance on the larger numerosities was considered. Furthermore, GK's improvements due to the colour and configuration manipulations fell within the range of the control sample. This suggests that displays with items in different colours, and displays with randomly placed items, benefit serial search with a limited spatial window, because (i) the individual colours lessen any load on spatial memory, and (ii) the locations of the items can be individuated more easily when the items are randomly positioned. This pattern held for both GK and the controls.

The main conclusion from this experiment is that GK's performance can largely be explained in terms of him having a limited attentional window when counting. It seems that when neurologically normal participants vision is limited to one object at a time, similar problems in counting arise to those found in GK. On the other hand, GK's estimation performance cannot be attributed to the operation of a limited spatial window of attention.

General discussion

GK was very poor at counting, but his counting was facilitated when cues were added to individuate the stimuli in the displays – with multi-coloured rather than single coloured items, with random patterns rather than configural displays. His errors on counting were also at best loosely related to the numbers of items present. On the other hand, GK was above chance at estimating the numbers of items present, and his estimation performance benefited when the items grouped – with single rather than multi-coloured items, with configural rather than random displays, and with collinear rather than circular elements.

Exact versus approximate number

At a first glance, our findings of severely impaired counting, but relatively preserved estimation fit with the idea of an impaired exact number system and a preserved approximate number system, following the distinction proposed by Feigenson et al.(2004). This account stresses that the exact number is abstract, being accessible from different modalities. However, GK remains able to count when stimuli are presented in modalities other than vision (e.g., the elevator counting task in the Test of Everyday Attention - Robertson et al., 1991). This indicates that there is no impairment of the exact number system per se; rather there is a deficit specifically in the visual coding of number. GK has highly impaired visual counting and there is no evidence even of accurate visual counting within the subitization range. As elaborated below, I attribute this visual counting problem to GK's impairment in visual attention and spatial representation following his bilateral parietal lesion.

Focused versus distributed attention

The differences between GK's counting and his estimating can be accounted for in terms of there being contrasting modes of visual attention. Focused attention, using a narrow attentional window, is adopted for counting; a more distributed attention mode, covering a wider spatial area, is adopted for estimating. Consistent with this proposal, GK's performance worsened with the same displays as those used for estimating, when he was asked to count the items present. He also performed worse at counting than at estimating when the two tasks were controlled for chance levels of responding, and his counting was very poor when the display durations were limited to the exposures used for estimating. These last results further indicate that, when in a focused attention mode, GK cannot explicitly use the information potentially available when a distributed mode of attention is employed.

Estimating and distributed attention

The results when estimating, indicate that patients with Balint's syndrome cannot be characterized as simply having an abnormally narrowed spatial window of attention (cf.

Thaiss & De Bleser, 1992). The data also indicate that such patients are able to attend to more than one element in a display, when a distributed mode of attention is adopted. This last conclusion is also supported by evidence on the perception of hierarchical stimuli in Balint's patients. Typically, such patients are biased to identify the local elements in such displays and they can be abnormally poor at identifying global forms (Karnath, Ferber, Rorden, & Driver, 2000; Shalev, Humphreys, & Mevorach, 2005). Nevertheless, there is evidence for implicit processing of the global forms since RTs to local elements can be speeded when the global forms are consistent rather than inconsistent with the local letter identities (Karnath et al., 2000, Shalev et al. 2005). Shalev et al. (2005) further showed that such patients could be cued to a hierarchical global form, if they had identified a solid large figure before the hierarchical stimulus is presented. Interestingly, this cueing effect dissipated rapidly, as the interval between the cue and the hierarchical form increased. This suggests that, although Balint's patients can adopt a distributed mode of attention, they find this state difficult to sustain and can quickly "collapse back" into using a narrow attentional window. This bias towards a narrow attentional mode can be speculated to be because of damage to neurons in the posterior parietal cortex with relatively large receptive fields that help to sustain a distributed mode of attention (c.f. Intriligator & Cavanagh, 2001)[4]. Due to their parietal damage, Balint's patients find this mode of attention difficult. Nevertheless, our data reveal that it is possible, and, when distributed attention occurs, the patients can be sensitive to effects of multiple-item grouping and inter-item similarity in visual perception.

Our results also indicate that GK was more sensitive to grouping between the items when he employed a distributed mode of attention (when estimating rather than counting).

---

[4] This is not to say that visually-responsive neurons in other cortical regions do not also have large receptive fields; there is (for example) strong evidence for this in infero-temporal cortex (Desimone & Ungerleider, 1989). However, to the extent that parietal neurons control the focus of visual attention, then loss of parietal neurons with large receptive fields will disrupt a distributed mode of visual attention.

Thus in the estimation task only, performance was improved with square patterns, when the elements could group by collinearity when in canonical patterns. This result is consistent with grouping by collinearity being modulated by attention (see also Freeman, Driver, Sagi, & Zhaoping, 2003); grouping by collinearity is stronger when the elements fall in an attended spatial region. This is not to say that same degree of grouping does not operate without attention (indeed GK's worse counting of items in configurations relative to randomly located stimuli, suggests some degree of pre-attentive grouping; see Gilchrist et al., 1996 for prior evidence), but it appears that grouping interactions are stronger when the elements are attended. This fits with an interactive view of visual processing in which top-down attentional activation combines with bottom-up activity from stimuli to facilitate visual processing (Cinel & Humphreys, 2006; Hochstein & Ahissar, 2002).

Counting and focused attention

The advantage GK showed for counting multi-coloured over single colour items was also mimicked in normal observers, when they were presented with a limited spatial window over the display. This provides converging evidence for GK having a narrow attentional window when he adopts a counting strategy, and, by contrast, him adopting a wider window in the estimation task. Also it should be noted that GK's counting of colour 'types' was better than his counting of individual item 'tokens' (see also Dehaene & Cohen, 1994).

This is consistent with GK having impaired location coding, with the result that he finds it difficult to tell if he has counted individual stimuli before (at least in a focused attention mode). Individual colour types, however, may be identified even with poor location codes, so that colour counting is advantaged. For example, colour types may be detected by activation in separate colour maps, within a 'colour space', that GK remains sensitive to, though he has difficulty recovering the location of any activity within each map. It appears that the parietal lobe is critical for the explicit recovery of such location codes, for separate objects (see Humphreys, 1998). This disruption to GK's explicit representation of the spatial locations of separate objects can help explain his very poor counting (when operating in a focused attention mode). For example, with poor spatial coding it may be difficult to fix attention accurately on individual object tokens, and it may be difficult to construct a spatial representation of those locations already attended. It can also help explain the rather puzzling finding that, although GK can operate in a distributed attention mode, he still shows no sign of subitization. This finding is puzzling because subitization itself likely depends on a mode of distributed attention. However, subitization may, in addition, require accurate coding of object locations, so that objects can be individuated (cf. Trick & Pylyshyn, 1993; 1994). Without individuation through accurate location coding, subitization is disrupted, despite GK being able to adopt a distributed as well as a focused mode of attention. An outline of the proposed relations between the mode of attention and the need for accurate spatial coding is provided in Table 1.

Table 1. Proposed relations between the task, the mode of attention, the requirement for accurate spatial encoding and GK's performance.

Task	Performance	Mode of attention	Spatial encoding
Subitizing	Severe impairment	Distributed	Required
Counting items	Severe impairment	Focussed	Required
Estimating	Mild impairment	Distributed	Not required
Counting Features	Preserved	Focussed	Not required

This suggests that GK's performance is relatively preserved when accurate spatial coding is not required, whilst he can adopt either a focused or a distributed mode of attention for counting and estimation tasks, respectively. When in a distributed attention mode, GK shows enhanced sensitivity to grouping, as well as sensitivity to statistics about the numbers of items present, but he may not have explicit information about the individual items in the group, including explicit information about their locations. I suggest that this characterizes the form of object coding that operates when attention is distributed across space (see also Shalev & Humphreys, 2002).

CHAPTER 3:

NEUROPSYCHOLOGICAL EVIDENCE FOR A DISSOCIATION IN COUNTING AND SUBITIZING.

Synopsis

There is a long and ongoing debate about whether subitizing and counting are separable processes. In the present chapter I report a single case, MH, who presents with a dissociation in subitizing and counting. MH was spared in his ability to enumerate small numbers accurately along with a marked inability to count larger numbers. I show that non-visual counting was intact and visual counting improved when a motor record of counting could be maintained. Moreover, when larger numbers of items were spatially grouped into 2 subitizable units, performance dramatically improved. However, colour grouping did not aid MH's performance, despite his being sensitive to colour segmentation. In addition, MH made more re-visits of inspected locations than controls, and he was less aware of a re-visitation being made. The data cannot be explained in terms of general working memory problems (verbal working memory was relatively spared), or general number comprehension problems (e.g. simple sums and counting of auditory items was intact); but they can parsimoniously be accounted for in terms of impaired visuo-spatial memory. The findings support the argument that at least some processes are specific to counting and are not required for subitization – in particular spatial coding and memory for previously inspected locations.

This chapter is currently in press in *Neurocase* (2010).

Introduction

Whether or not subitizing and counting rely on distinct processes is an ongoing debate - A possibly stronger argument for a qualitative difference between enumerating small and large numbers would come from evidence demonstrating distinct effects of contrasting factors on ‘subitizing’ and ‘counting’. In the present chapter I report a single case study of a patient who, like others noted above (see Chapter 1 – Neuropsychological evidence), had a spared ability to count small numbers accurately along with a marked inability to count larger numbers (Experiment 3.1). Unlike other cases, I show that non-visual counting was spared and visual counting improved when a motor record of counting could be maintained. Other experiments explored the factors influencing counting. Performance improved dramatically when larger numbers of items were spatially grouped into 2 subitizable units (Experiment 3.2) while similar effects did not occur with colour-grouping (Experiment 3.3). This suggests a sensitivity to the load of stimuli on visuo-spatial memory. Enumeration also improved when MH was forced into a serial counting mode by tapping each item in order to count (Experiment 3.4), The data cannot be explained in terms of general working memory problems (verbal working memory was relatively spared), or general number comprehension problems (e.g. counting of auditory items was intact). In a final experiment (Experiment 3.5) I tested MH’s search and assessed both whether potential target locations were re-visited and whether MH was aware when this occurred. MH made many more re-visits than controls, while also showing impaired awareness when re-visits took place. I suggest that poor spatial coding and visuo-spatial memory are responsible for the error prone counting behaviour, with these processes being specific to counting. Poor monitoring of search is insufficient to account for the pattern of deficits.

MH: Case Report

MH was 53 years old at the time of testing. He suffered an anoxic incident at age 42, resulting in right side muscle weakness and raised sensory thresholds. He had no problems with walking and could still use both hands. For details of a clinical assessment, see Riddoch et al. (Riddoch et al., 2004). A recent MRI scan (2006) showed disseminated lesions consistent with the anoxic aetiology (see Figure 13). Sub-cortical atrophy was apparent in bilateral lentiform nuclei and the heads of the caudate nuclei. Cortical lesions were evident in bilateral posterior parietal regions, but were more pronounced on the left side (including the occipital-parietal borders, intraparietal sulcus and superior parietal lobe). A smaller lesion was also present in the left middle frontal gyrus.

In a series of standard tests, MH scored full marks on counting tones in the Elevator subtest taken from the Test of Everyday Attention (Robertson et al., 1991). In a verbal test of simple addition, using sums totalling under 20 (e.g., 11 + 5 = ??), MH demonstrated perfect accuracy. He had a Forward digit span of 5 and a Backward digit span of 4. In a cancellation test designed to detect visual neglect, MH showed no spatial asymmetry across the page, cancelling 47/50 of the targets present. On the Corsi block tapping test (Corsi, 1972), MH presented with a very poor visuo-spatial memory span of 2. In order to measure his spatial tagging and spatial memory performance, I also administered an “Invisible star Cancellation” test (Wojciulik, Husain, Clarke, & Driver, 2001), in which a piece of carbon paper and a blank sheet were attached to the back of the star cancellation task from the Behavioral Inattention Test (Wilson et al., 1987), and responses are made with the back of a pen (leaving no visible mark - marks are assessed on the blank paper underneath the carbon paper). MH again showed a low asymmetry neglect score (-4: omitting 4 stars on the left side of the page – ipsilesional to the main site of cortical damage), but the invisible version did result in a very high score for re-visitations (22 out of the 46 stars cancelled, asymmetry score: -6). Two age matched controls performed the same task and revisited 4 and 1 cancellation respectively. In a span version of the moving object tracking task (Pylyshyn & Storm, 1988), MH was able to track on average about 1.5 moving objects. Five age-matched controls scored a mean of 3.5 tracked objects (SD 0.25) (Hulleman & Humphreys, unpublished).

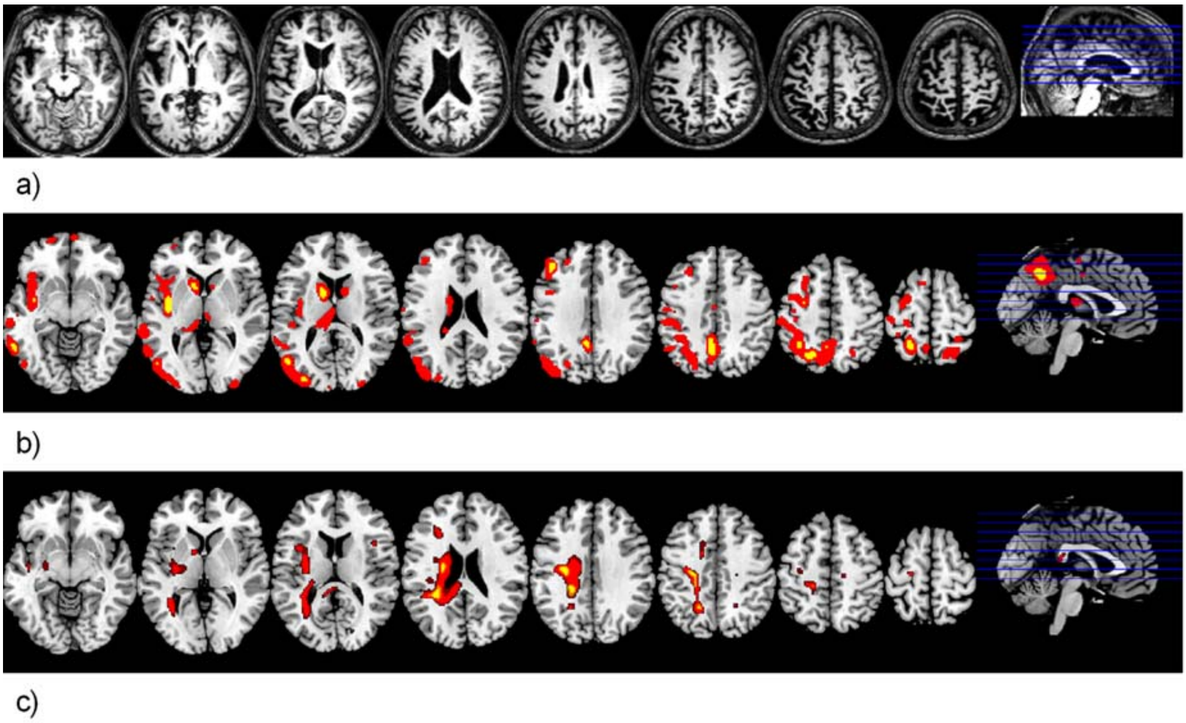


Figure 13. a) Original normalized T1 image. b) Grey matter lesion created in SPM5 (http://www.fil.ion.ucl.ac.uk/spm/software/SPM5) and added as an overlay on to a standard multi-slice template in MRIcron. T1-weighted images were segmented in grey matter, white matter, and cerebro-spinal fluid (CSF), and the resulting tissue classes images were normalized without modulation (i.e., to compensate for the effect of spatial normalization). Images were smoothed with a Gaussian kernel of 2 ×2 ×2 mm. SPM stats: one sample t- test with 3 covariates: healthy grey matter (201 brains aged 40+) vs patient grey matter, age & sex. Red areas denote uncorrected significant results, yellow areas are FWE corrected with p=0.05 and an extent threshold specifying that only significant blobs containing ≥40 voxels be included in the lesion. c) White matter lesion created in SPM 5, using identical method, with segmented white matter instead of grey matter.

Experiment 3.1: Basic visual enumeration of random dot patterns.

In this experiment, I assessed MH's performance on visual enumeration of randomly placed dots. I also tested 8 healthy participants (average age 64.6, SD= 6.1) on the same task to assess normal control performance levels and two unilateral parietal patients. These patients were 72 and 52 years old. One had damage to left inferior parietal cortex and one to right inferior parietal cortex. Unlike MH, who did not present with symptoms of spatial neglect, both unilateral parietal patients had some aspects of neglect. One (right parietal) missed stimuli on the left in cancellation tasks; the other patient (patient RH; Kitadono & Humphreys, 2007) missed left side letters in reading and with shorter stimulus presentation.

Method

This experiment was programmed and run using E-prime 1.1 software (Schneider, Eschman, & Zuccolotto, 2002). The displays were presented on a black background on a 17 inch monitor with 1024x768 pixel screen resolution. Each participant was positioned approximately 65 cm from the screen. The stimuli consisted of 1 to 9 grey dots (RGB: 190,190,190), which were drawn randomly within the centre 500x500 pixels of the screen (14.4 ˚ visual angle). The dots had a diameter of 25 pixels (1.4 ˚ visual angle) and any two dots were separated from each other by a minimum distance of one dot diameter.

One trial started with the presentation of a fixation cross in the centre of the screen for a duration of 1000ms. Next, the dot display appeared and remained on the screen for an unlimited duration until a response was made. Participants were instructed to enumerate the dots in this display as accurately and quickly as possible. As soon as they felt they knew the correct response, they had to press the space bar and simultaneously spoke their response. When the spacebar was hit, the dot display disappeared and was followed by a blank screen, where the experimenter entered the reported number using the numeric key pad (for a similar method, see Atkinson, Campbell, & Francis, 1976; Watson & Humphreys, 1999; Watson & Maylor, 2006). Accuracy and reaction times (RTs) were recorded.

Both MH and the control participants completed 6 blocks in one session, with each block containing 45 randomly ordered trials (5 per numerosity). This resulted in a total of 30 trials per numerosity (1-9).

Results

Across numerosities 1-4 MH made no errors in enumeration (Figure 14). His performance fell within 2 standard deviations of the average of the healthy controls (mean control= 99.9% correct, SD= 0.3), and did not differ from the patient controls (p= .249, Fisher's Exact Test relative to the worst of the two unilateral patients who scored 99.2% and 98.3 % correct respectively).

In contrast, across the counting range[5] MH enumerated only 44.2 % of the trials correctly. This clearly fell outside of the normal control range (mean = 98.4, SD= 1.3), and was also significantly worse than the poorest performance of the two patient controls (p< .001, Fisher's Exact Test - average 89.2 and 85% correct). The errors MH made ranged from overestimating by 1 cardinality to underestimating by 3. The errors were mainly underestimations (95.4 % of errors), and of those the majority were underestimations of only 1 cardinality (74.7%).

---

[5] The counting range was considered to involve the numbers 5-8 here, since we used a maximum 9 item display and responses to 9 items may be affected by guessing (following previous enumeration studies, e.g. Trick & Pylyshyn, 1993)

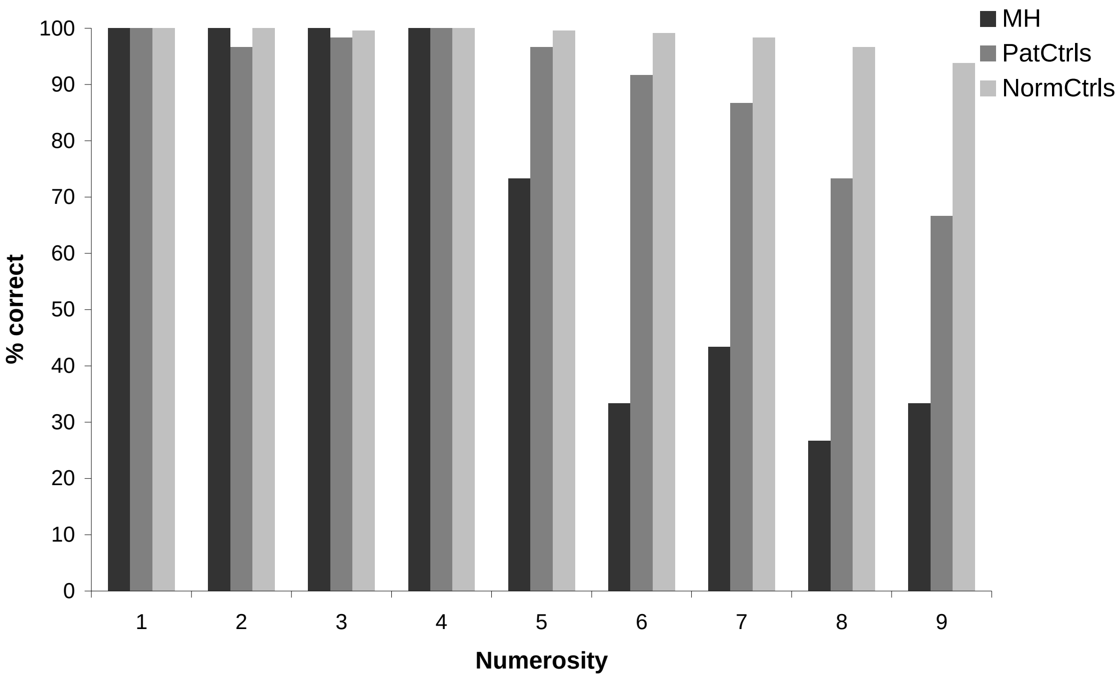


Figure 14. Performance on counting randomly positioned dots, accuracy scores for MH and the average score of 2 unilateral parietal patients and 8 healthy controls.

In order to assess enumeration times (see Figure 15), RT slopes were calculated across the subitizing and counting ranges using linear regression, with numerosity as the independent factor. Inspection of MH's RTs suggested a discontinuation at numerosity 4, therefore I will consider the subitizing range to be numerosities 1-3 and the counting range 5-8. For the subitizing range, MH had an RT slope of 178.6 ms per item, which fell outside 2 standard deviations (SD= 32.22) of the average slope for the controls (mean= 35.20 ms per item). It was however similar to the slopes of the patient controls (150.8 and 276.25[6] ms per item). MH's RTs were compared to those of the worst control for correct responses to numerosities 2 and 3 in a univariate analysis (trials were treated as subjects). There was no reliable

---

[6] This slope was calculated on numerosities 2 and 3 only due to this patient demonstrating unreliable RTs for numerosity 1 (SD= 400.29) compared to numerosities 2 (SD= 165.18) and 3 (SD= 248.52). This was corroborated by Levene's test of homogeneity of variance in a comparison of numerosities 1 to 3 (F(2,82)= 4.194, p= .018).

difference between the two patients (F(1,109)= 1.139, p= .288). And no interaction between the patients and the actual numerosity (F(1,109)= .748, p= .389).

For the counting range (5-8), MH's RT slope (781.49ms per item) again fell outside of the normal control range (mean = 263.64 ms per item, SD= 115.05), as well as being steeper than the patient control slopes (504.7 and 363.6 ms per item). MH's RTs were compared to those of the worst control for correct responses to numerosities 5,6,7,8 in a univariate analysis (trials were treated as subjects). There was a significant difference between the two patients (F(1,140)= 230.950, p< .001), as well as an interaction between the patients and the numerosity (F(3,140)= 3.623, p= .015) indicating the steeper slope for MH compared to the control patient.

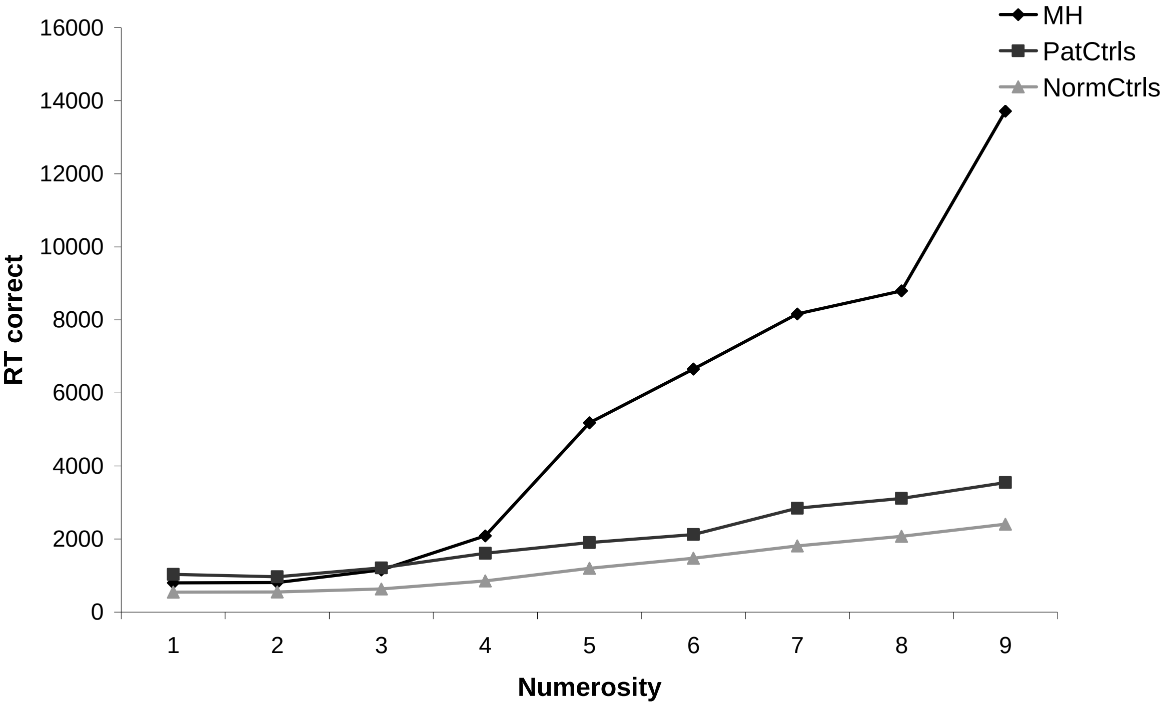


Figure 15. Correct RTs (ms) for MH and the mean of the two parietal control patients as well as the average of 8 healthy control participants as a function of the numerosity presented.

Although MH showed significant RT increases per extra item enumerated for both the subitizing and counting range, the extra cost per item on the counting range was considerably larger than on the subitizing range (178.6 vs 781.49 respectively). This was validated by a univariate analysis (treating trials as subjects) on RTs with two factors: Size (small (sizes 1-3) vs. large (sizes 5-7) numbers) and Numerosity (items 1-3 vs. 5-7). We found significant main effects of Size (F(1,129)= 158.613, p< .001) and Numerosity (F(2,129)= 7.753, p< .001). There was also a significant interaction between size (large or small numbers) and numerosity (F(2,129)=5.067, p= .001), confirming the steeper slope for counting than for subitizing. The controls also showed a distinct dog leg function, in a similar analysis, with a significant interaction between numerosity and size (F(2,14)= 22.483, p<.001).

Discussion

MH demonstrated a strikingly impaired ability to enumerate accurately in the counting range (> 4), with fewer than half of the trials for these larger numerosities being enumerated correctly. In addition, when his response was correct, MH was very slow, and demonstrated considerably higher RT costs than normal as a function of each item that needed to be enumerated. In contrast, his enumeration performance on the smaller numerosities in the subitizing range was flawless. And although his RT slope in the subitizing range was somewhat steeper than that of controls, it was similar to the two unilateral parietal patient controls, in line with an overall slowing of RTs after brain damage. Importantly however, the cost per item in the subitizing range was considerably lower compared to when MH correctly enumerated in the counting range, consistent with a qualitative shift in performance for small versus large displays. For the counting performance, MH demonstrated a larger cost per item both compared to the healthy controls as compared to the patient controls, suggesting a deficit over and above general slowing of RTs after brain damage.

When comparing MH’s reaction time slopes with the controls, the ratio for the subitizing range (~ 5:1) is actually larger than his slope ratio for counting (~3:1). However, this should not be interpreted as MH having a more preserved counting performance. When considering MH’s accuracy data, it is clear that his counting of more than 4 items is severely impaired (correct counting in fewer than half the trials), his RT slope was calculated on the correct responses only, and it should be noted that his severe impairment in counting meant he would often start counting and then lose track, and make an educated guess. This strategy also explains the faster RTslope on the counting range.

Since MH had no problem enumerating auditory items (see Case Report), and since he was still above chance in the counting range, his impaired counting performance cannot be explained in terms of poor number comprehension or in terms of other processes that could selectively affect counting (e.g., the keeping track of larger numbers). Rather the data point to a problem that is specific to when MH has to assimilate larger numbers of visual elements. One critical factor here might be an impairment in visuo-spatial short-term memory. MH’s performance on the Corsi block task was poor, as was his ability to track moving items, and both of these may reflect a limitation in visuo-spatial short-term memory. In Experiment 3.2, the locations of the random dots were manipulated in order to lower the load on visuo-spatial memory. Would this facilitate counting?

Experiment 3.2: Visual enumeration of items in 2 spatially defined sub-units.

In this experiment, the displays were split up in a lower an upper visual field, each containing subitizable numbers of dots.

Method

The experimental set-up and procedure was identical to Experiment 3.1, except for the lay-out of the random dots on the display. Rather than randomly positioned across the entire display, the display contained 2 invisible rectangles (size 512x200pixel – 14.5˚ x 5.7˚ visual angle). These were separated along the vertical axis by 4.8˚ (168pixel), with equal distances from the top and bottom of the screen, and centered horizontally, with equal distances to the sides of the screen. This subdivision allowed for a manipulation of spatial grouping: the dots were drawn in the upper and/or lower visual field. A further manipulation to ensure that no more than 2 spatial groups would occur by chance, was to draw the dots (within a group) equidistant from each other. This was done by starting from a centre location, and then selecting a random location on a 85pixel (2.5˚) radius. The next location was subsequently determined on a random angle from the last one (again fixed distance of 2.5 ˚), and so on until all dot locations were determined. There were imposed constraints to ensure dots would not overlap or fall within 75pixel (2.2˚) distance from any of the previously chosen locations, and all locations stayed within the predetermined area (upper or lower field).

There were 7 numerosities (2 to 8) x 2 grouping conditions. The dots could either all fall within the upper or lower visual field, or they could be split in subitizable units (≤ 4) over the two areas. For examples of the displays used, see Figure 16. The instructions and procedure were the same as in Experiment 3.1. Only MH completed this experiment across 2 sessions (with a 1 week interval). There were 4 blocks in one session, with each block containing 56 randomly ordered trials. This entailed 4 trials per numerosity in the split-field condition and 2 trials per numerosity where all dots were in the lower half and 2 trials in the upper half condition (4 per numerosity). This resulted in a total of 32 trials per numerosity (2-8) per condition (split-field or grouped).

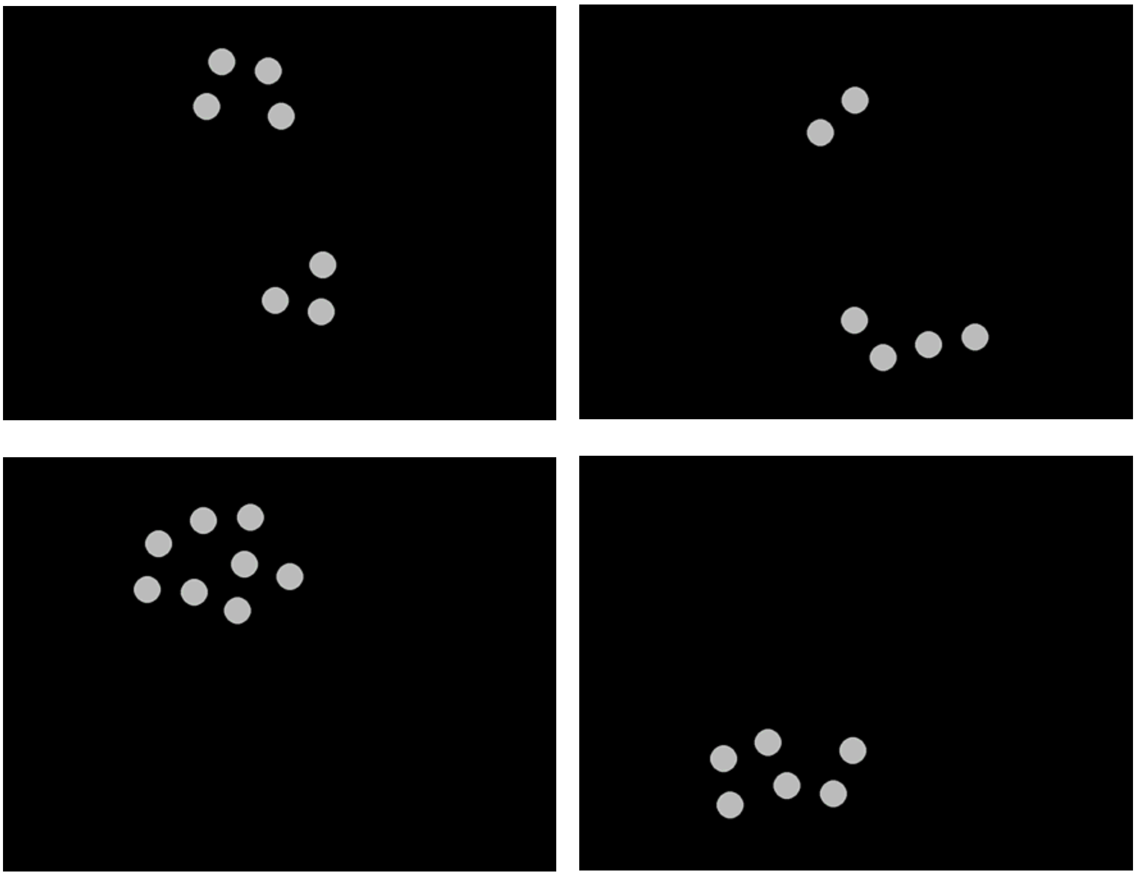


Figure 16. Examples of the stimuli used in Experiment 3.2, where the numerosities were presented either divided over 2 visual fields (top), or all within one visual field (bottom).

Results

As in Experiment 3.1, MH’s accuracy was perfect for enumerating numerosities up to 4, both in the split-field and grouped conditions (see Figure 17). However, when there were more than 4 dots present, and all of the items were presented together in either the top or bottom visual field, the results from Experiment 3.1 were replicated, with MH responding correctly on fewer than half the trials (mean % correct= 46.9). There was no reliable difference between his performance here compared to in Experiment 3.1, when all the dots were spaced out over the visual field (p= .468, Fisher’s exact test). However, when the dots were presented in two subitizable units in two separate visual fields, his accuracy dramatically increased (mean % correct= 75), this difference was significant (p< .001, Fisher's exact test). Even though MH's accuracy was not perfect in this split-field condition, it is important to note that all the trials where MH made an incorrect response contained a subgroup of 4 items in one of the fields. The data on enumeration times in Experiment 3.1 indicated that MH's subitizing limit was nearer to 3 than 4 (see Figure 14, Experiment 3.1). In the trials which contained fewer than 4 items in the subgroups, MH's accuracy was 100%.

The errors MH made ranged from overestimating by 2 items to underestimating by 2. For the grouped condition, 58.8% of errors were underestimations, while for the split-field condition underestimations comprised 84.4% of errors made.

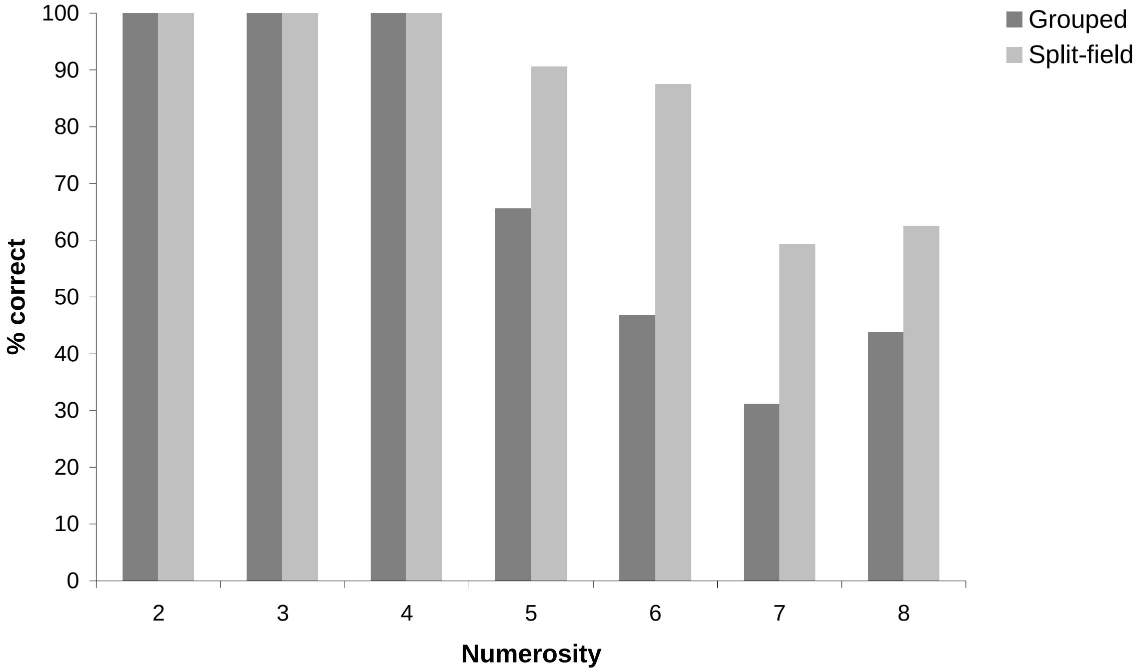


Figure 17. MH's performance when enumerating randomly positioned dots, placed either together in one visual field, or split over 2 visual fields in subitizable units.

RTs for MH's correct responses are presented in Figure 18. RT slopes for the subitizing range (2-3) were 171 and 233 ms per item for the one field and split-field conditions; slopes for the counting range (5-8) were 1712 and 859 ms per item for the one field and split-field conditions respectively. A between-subjects analysis was conducted on the raw RTs for correct responses, with the factors being Spatial grouping (1 vs 2 visual fields), Size (Small vs Large) and Numerosities (2,3 – 5,6). There were overall significant effects of Spatial grouping (F(1,213)= 19.914, p< .001), with faster response times in the split-field condition, effects of Size (F(1,213)= 191.214, p< .001), with responses to small magnitudes faster than to larger magnitudes and effects of Numerosity (F(1,213)= 9.875, p= .002). In addition, the interaction between Spatial grouping condition and Size (F(1,213)= 24.515, p< .001) was significant. There were no other reliable interactions.

When numerosities up to 4 were considered, where MH demonstrated perfect accuracy, I also found faster RTs for split-field numerosities than for grouped dot displays (F(1,186)= 5.967, p= .016), as well as an effect of numerosity (F(2,186)= 45.447, p< .001). There was also a significant interaction between the condition and the numerosity (F(2,186)= 9.6, p< .001). However, with numerosities 2 and 3, only a significant effect of the numerosity was found (F(1,124)= 6.546, p= .012), but no significant effect of the spatial grouping (F(1,124)= .851, p= .358) and no interaction (F(1,124)= .152, p= .697). This demonstrates that grouping into two spatially distinctive units makes no difference in the speed to enumerate small numbers up to 3, but does help deliver a faster performance on displays of 4 dots and over. In other words, enumerating 4 dots in one visual field was harder for MH than enumerating 2 groups of 2 dots or a group of 3 dots with an extra separately placed dot. This confirms the initial analysis where the limit of MH's subitizing range was considered to be 3 rather than 4 items.

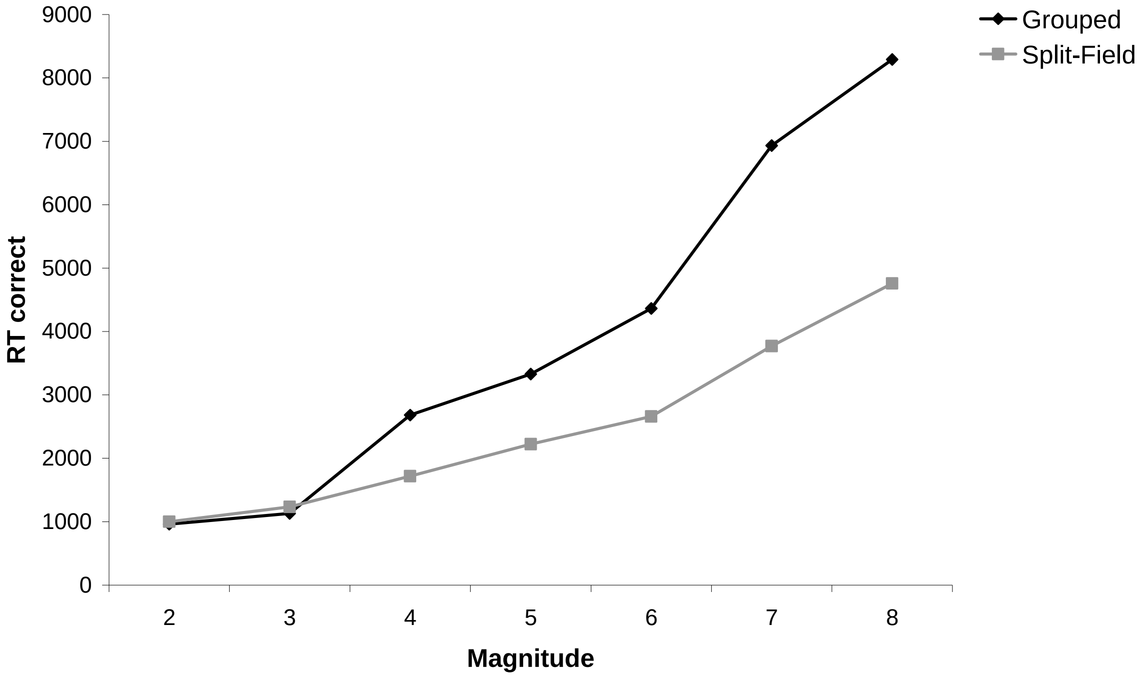


Figure 18. Correct RTs (ms) for MH, when correctly enumerating dots, either in 2 visual fields or grouped in the top or bottom part of the screen.

A final comparison was made between the grouped (one field) condition and the original first experiment (where items covered both fields, as in the split field condition here). This revealed no reliable difference in RTs (F(1,259)= 1.033, p= .310), demonstrating that the beneficial effect of splitting the display into subitizable groups cannot be accounted for by the wider spacing of the items.

Discussion

I replicated the results from Experiment 3.1, with MH demonstrating perfect performance across the subitizing range in contrast to him being seriously impaired at counting. This experiment also demonstrated that when the numerosities were spatially grouped into two subitizable units, MH's performance improved dramatically in the counting range. Even though MH's accuracy was not perfect in this split-field condition, he was both significantly more accurate and faster when the display consisted of two subitizable patterns compared to when all the dots were presented grouped closely together in one part of the display. Furthermore, when only considering displays containing subgroups of fewer than 4 elements, MH's counting performance was error-free. No differences in performance (accuracy or RT) were found between the closely grouped condition in one visual field and the performance in Experiment 3.1, demonstrating that this is not just an effect of average spacing of the elements.

Experiment 3.3a: Visual enumeration of items in 2 colour-defined sub-units.

In Experiment 3.3a, I assessed whether the advantage of grouping the display into subitizable units (Experiment 3.2) depended specifically on spatial grouping, or whether grouping by another feature (i.e. colour) resulted in the same improvement.

Method

The experimental set-up and procedure was identical to Experiment 3.1, except for the colouring of the dots in the display. There were 2 conditions: a heterogeneous condition, where there were two groups of dots: green (RGB: 0, 128, 0) and red (RGB: 255, 0, 0), and a homogeneous condition, where the dots were all coloured in the same colour (red or green). In the heterogeneous condition, the numbers of red and green dots were always subitizable units, e.g. 4 and 2 to make 6. The colours were assigned at random, so that the items did not form spatial groups of separate colours. Examples of the displays used can be found in Figure 19.

The instructions and procedure were the same as in Experiment 3.1, MH completed this experiment across 2 sessions (with a 1 week interval). There were 4 blocks in one session, with each block containing 56 randomly ordered trials. This entailed 4 trials per numerosity in the heterogeneous condition and 2 trials per numerosity where all dots were green and 2 trials where they were red. This resulted in a total of 32 trials per numerosity (2-8) per condition (heterogeneous or homogeneous).

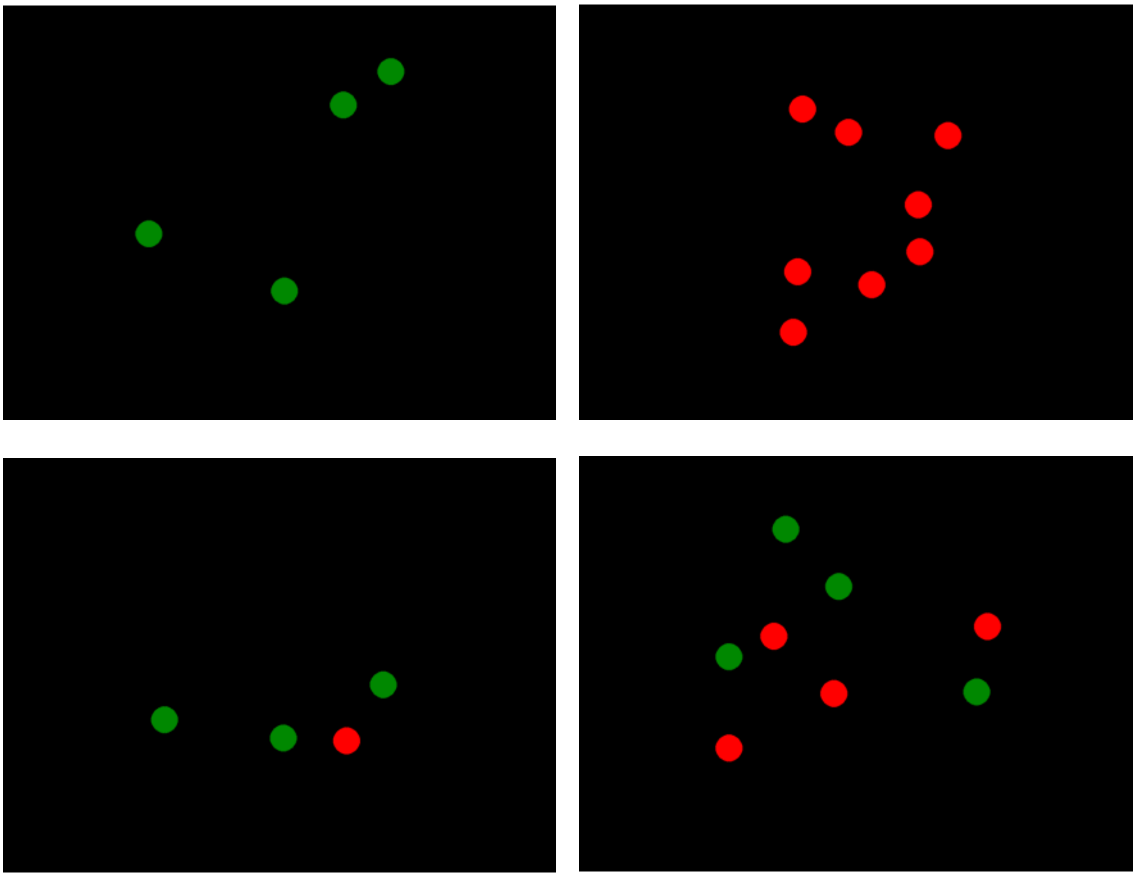


Figure 19. Examples of the stimuli used in Experiment 3.3a, where the numerosities were presented in 2 subitizable units (defined by colour), or in homogeneous displays of 1 colour.

Results

As in Experiment 3.1 and 3.2, MH's accuracy was near perfect for enumerating numerosities up to 4, both with heterogeneous colours (only 1 error on a display of 4 elements) and in the homogeneous colour condition (see Figure 20). When there were more than 4 dots present, and the dots were all in one colour (either red or green), MH responded correctly on just over half of the trials (mean % correct= 54.9). When the dots were presented in two subitizable units in two different colours, he responded correctly on 58.6% of the trials. The difference between the heterogeneous and homogeneous displays was not statistically significant (p= .529, Fisher's Exact test).

The errors MH made ranged from overestimating by 2 items to underestimating by 2. For the homogeneous colour condition, 71.7% of errors were underestimations, while for the 2 colour condition this was 83% of the errors made.

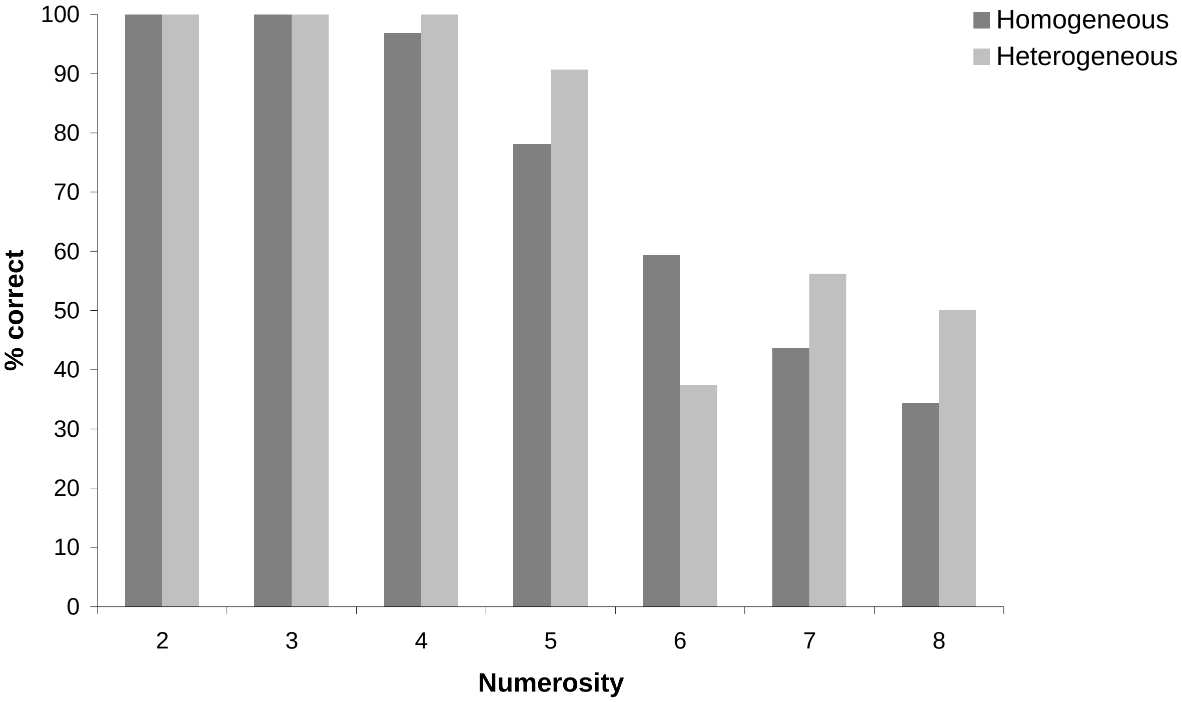


Figure 20. Accuracy when enumerating displays made up of randomly positioned green or red dots, versus randomly positioned mixed green and red dots.

The mean RTs for MH's correct responses are presented in Figure 21. RT slopes for the subitizing range (2-3) were 354 and 388 ms per item for the homogeneous and heterogeneous conditions respectively; slopes for the counting range (5-8) were 1496 and 1485 ms per item for the homogeneous and heterogeneous conditions respectively. The raw RTs for correct trials were entered into a between-subjects ANOVA with the factors being Colour grouping (1 vs 2 colours), Size (small vs large) and Numerosity (2,3 – 5,6). There was no reliable effect of colour grouping (F(1,205)= 2.480, p= .117). There was only an overall significant effect of size (F(1,205)= 178.079, p< .001).

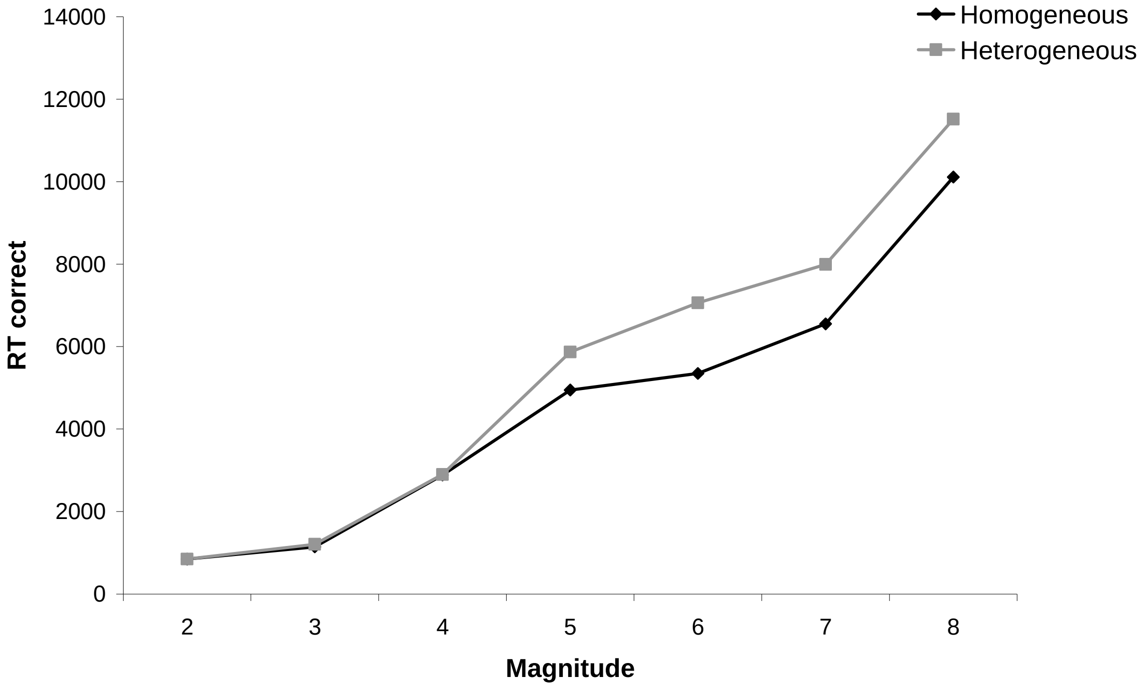


Figure 21. Correct RTs (ms) when MH enumerated displays of green or red dots, versus mixed green and red dots.

Discussion

No advantage was found for splitting the numerosities into subitizable units defined by colour. This indicates that MH was unable to use colour segmentation as a means to group the elements into subitizable units. In contrast to this result, Riddoch and colleagues (2004) reported that MH had a good ability to detect a target defined by a local colour difference relative to the background. Hence MH does not have a problem in colour segmentation per se, but he does when he has to use colour to guide enumeration. The data suggest that spatial grouping still dominates, and overrides any colour effects. This is consistent with the argument that subitizing and counting are inherently spatial processes, operating on a map of stimulus locations (Watson & Maylor, 2006).

Experiment 3.3b: Effects of Colour and spatial grouping on visual enumeration

Experiment 3.3b tested whether there were beneficial effects of colour segmentation on counting, but when the colours were spatially segregated so that different spatial groups could be formed.

Method

In this experiment, spatial grouping between the colour groups was manipulated. There were always 2 subitizable colour groups, and this time the spacing between the elements was held constant, so as to control for the accidental spatial grouping that could have occurred in Experiment 3.3a. The dots were positioned equidistant (see Method Experiment 3.2) in the centre of the screen (500x500 px area – 14.4° visual angle). The total number of dots in a display always consisted of 2 subitizable colour sub-groups (red and green – see Experiment 3.3a). This time either the colour groups also formed spatial groups (Figure 22a), or the colours were interleaved, therefore disrupting spatial grouping of the two colour groups (Figure 22b).

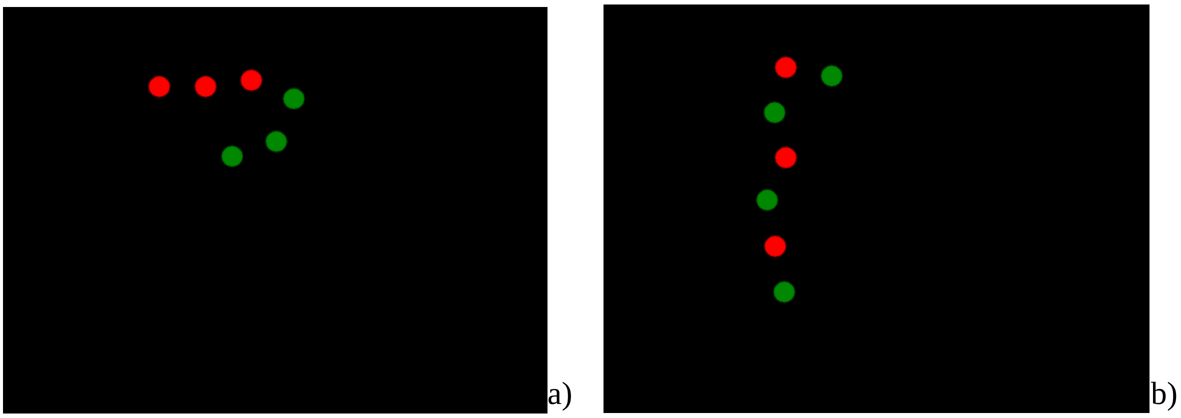


Figure 22. Examples of displays in Experiment 3.3b.

Results

As before, MH's accuracy was near perfect for enumerating numerosities up to 4, in both conditions (1 error on numerosity 4) (see Figure 23). When there were more than 4 dots present, and the colour groups formed spatial groups, MH responded correctly on 89.6% of the trials. However, when the colours were interleaved and did not form spatially defined subgroups, performance dropped to 65.6% correct. This difference proved statistically significant (p< .001, Fisher's Exact test). There was no difference in accuracy between MHs performance in the interleaved and hetereogeneous conditions in Experiment 3a (where there was no equal spacing between the elements) (p= .332, Fisher's Exact test).

The errors MH made in this experiment ranged from overestimating by 1 item to underestimating by 2. In the colour grouped condition, 70% of errors were underestimations, while for the colour interleaved condition underestimations comprised 82.4% of the errors made.

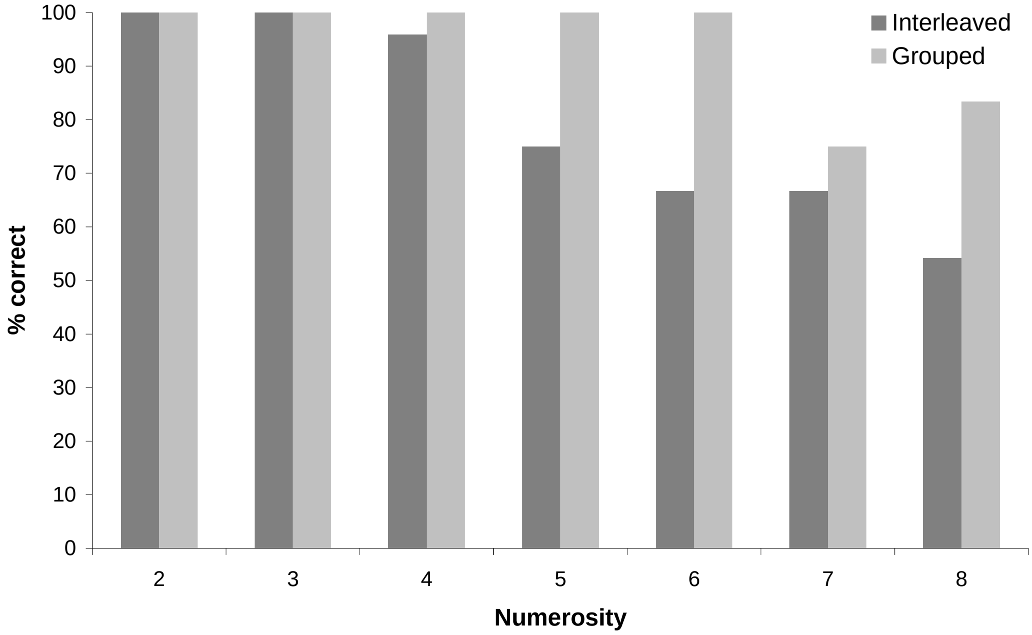


Figure 23. Accuracy when enumerating displays made up of mixed green and red dots where the colour groups were also spatially defined, or not.

RTs when MH responded correctly are presented in Figure 24. RT slopes for the subitizing range (2-3) were 296 and 274 ms per item for the spatially and colour grouped vs colour grouped only conditions respectively; slopes for the counting range (5-8) were 961 and 1351 ms per item for the spatially and colour grouped vs colour grouped only conditions respectively

The raw RTs for correct trials were entered into a between-subjects ANOVA with the factors being spatial Colour grouping (grouped vs interleaved), Size (Small vs Large) and the Numerosity (2,3 – 5,6). There was a significant effect of Spatial colour grouping (F(1,164)= 65.646, p< .001), as well as Size (F(1,164)= .15.747, p< .001) and Numerosity (F(1,164)= 7.668, p= .006). There were also reliable interactions between spatial Spatial grouping and Size (F(1,164)= 66.526, p<.001) and between Spatial grouping and Numerosity (F(1,164)= 9.818, p= .002). The 3-way interaction was also reliable (F(1,164)= 10.159,p=.002).

Taking performance in the subitizing range only (2-3), there was no reliable difference between the two grouping conditions (F(1,90)= .049, p= .825). For the counting range (5-6), MH was significantly slower for displays that could only be grouped by colour, in contrast to the when there was both spatial and colour grouping (F(1,74)= 54.970, p< .001).

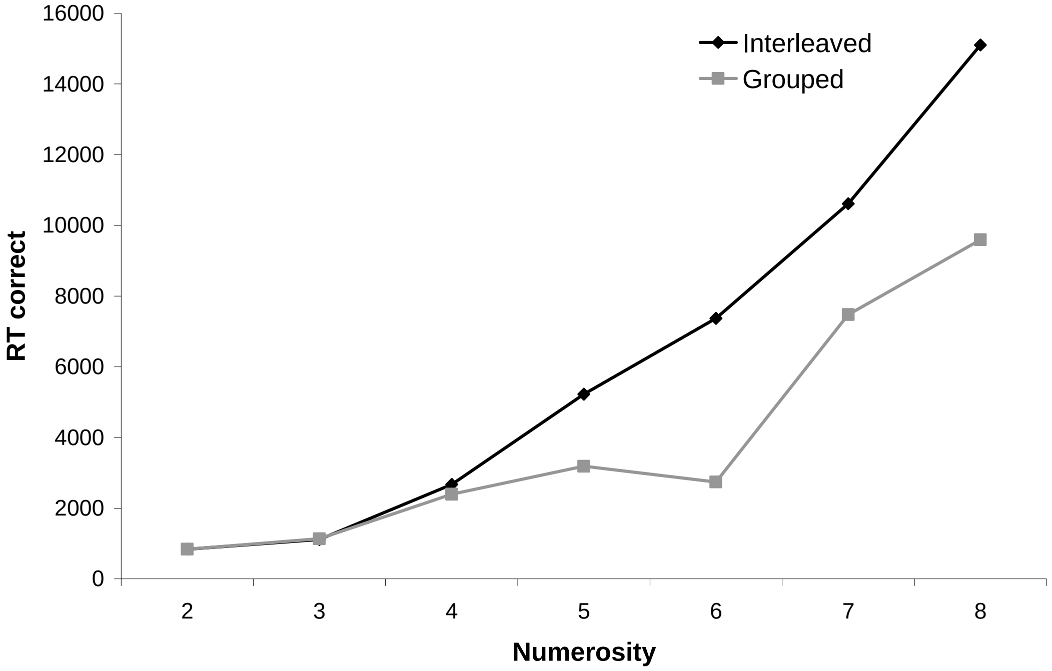


Figure 24. Correct RTs (ms) when MH enumerated displays of green and red dots, which additionally formed spatial subunits or not.

Discussion

Experiment 3.3 demonstrated that, although MH was not helped by colour grouping in itself (Experiment 3.3a), he did benefit when the colours formed spatially separate subitizable units. This indicates that, although MH can use colour segmentation (Riddoch et al., 2004), spatial grouping rather than colour grouping is used for counting. (Watson & Maylor, 2006). With spatially grouped colours, MH's performance improved in the counting range but there was no effect within the subitizing range.

Experiment 3.4: Forced serial counting.

One interpretation of the data from Experiments 3.2 and 3.3 is that MH relies on subdividing the display into subitizable units in order to count. However, when the display does not group into smaller (subitizable) units, MH loses track of where he has been and which parts he has already counted. If this is the case, then performance might be improved if MH is able to use another form of stimulus coding to keep track of the items. This was tested here by requiring MH to gently tap each dot in order to count the total number of dots in a serial manner. If MH can use a motor representation of where he has explored, then the tendency to re-trace counted items may reduce and MH may be more accurate at enumerating large display sizes.

Method

Rather than using a computer task, a paper-based task was used; this enabled MH to tap each dot in succession with the back of a pen as he counted the total number of dots present. The stimuli were shown on A5 pieces of paper. The dots were drawn with the same algorithm as in Experiment 3.2, creating equidistant random dot patterns (see the Method for Experiment 3.2). This was done to eliminate any spatial grouping that can occur by chance in a completely random display. MH’s task was to count the total number of dots present on the paper. Responses were noted and RTs were recorded by stopwatch. There were 3 conditions, which were administered sequentially over 6 sessions (with 1 week interval). In the first condition, MH was instructed to tap each dot with the back of a pen in order to count the total number of dots present. In the second condition, MH was instructed just to count, without touching (as in Experiments 3.1- 3.3). In the final condition, MH again was instructed to count the dots while tapping each dot sequentially, but this time was wearing headphones delivering white noise in order to mask any sounds of the tapping. This was done to ensure that MH was not counting the sound of the taps, but instead was using the tapping as a visuo-motor aid. MH performed a total of 20 trials per numerosity, per condition.

Results

In all three conditions MH made no errors when enumerating displays of up to 4 dots (see Figure 25). In contrast there was a relatively high error rate in all conditions across the counting range (5-8), with an average of 60% correct in the no tapping condition, 83.75% correct when tapping each dot and 86.25% correct when tapping each dot while listening to white noise. The difference between the no-tapping and tapping conditions was statistically reliable, both for standard tapping (p= .001, Fisher's Exact test) and for tapping in white noise (p< .001, Fisher's Exact test). There was no difference between the two tapping conditions (p= .825, Fisher's Exact test).

The errors MH made in this experiment ranged from overestimating by 2 items to underestimating by 2. In the 'no tapping' condition, 86% of errors were underestimations, in the 'tapping' condition, 76% were underestimations and in the 'tapping with noise' condition, this was 50% of the errors made.

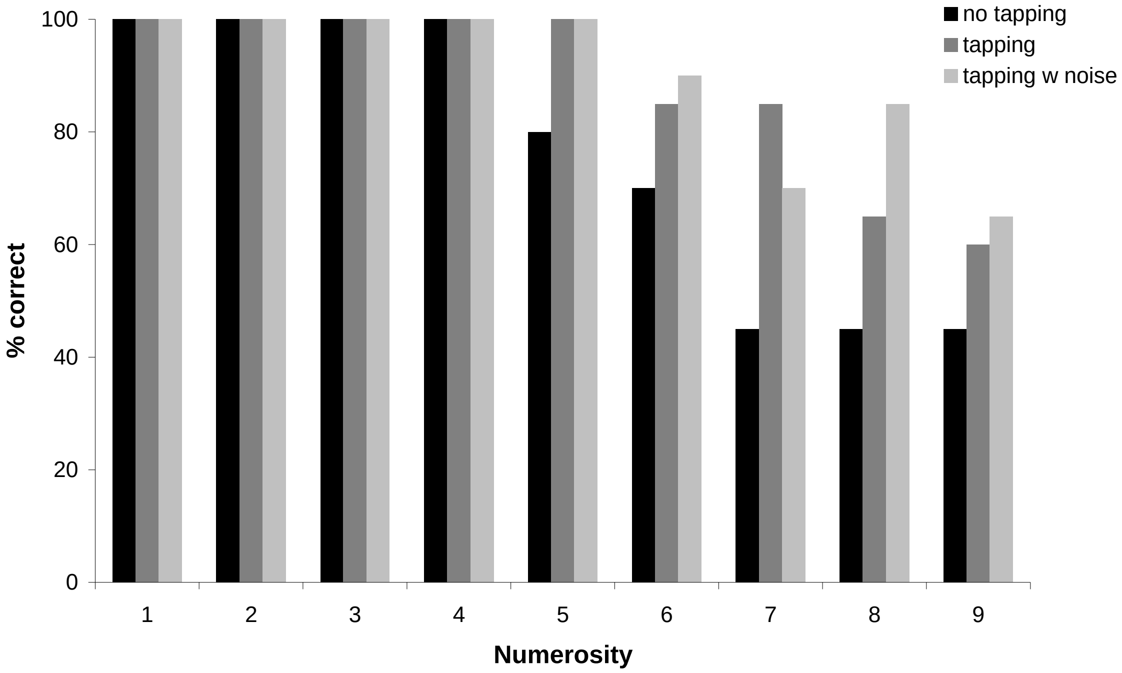


Figure 25. Accuracy when enumerating random dot displays, with MH not touching the stimuli, compared to when he tapped each dot successively in order to count (either while listening to nothing or white noise to mask the tapping sounds)

RTs when MH responded correctly are presented in Figure 26. RT slopes for the subitizing range (1-3) were 0.143s per item[7] in the “No tapping” condition, 0.345 s per item in the “Tapping” condition and 0.523 s per item in the “Tapping with noise” condition. For the counting range (5-8), RTslopes were 0.536 s per item in the “No tapping” condition, 0.755 s per item in the “Tapping” condition and 0.776 s per item in the “Tapping with noise” condition.

A between-subjects analysis was conducted with the factors being Tapping condition (no tapping, tapping, tapping with noise), Size (Small vs Large) and Numerosity (1,2,3 – 5,6,7) on the raw RTs for correct trials. A reliable effect of the Tapping condition was found (F(2,307)= 36.401, p< .001), with MH being slower when he was tapping the dots compared to when he was not. There were also reliable effects of Size (F(1,307)= 613.864, p< .001) and Numerosity (F(2,307)= 26.581, p< .001). There were also significant interactions between Tapping condition and Size (F(2,307)= 16.332, p< .001) as well as between Size and Numerosity (F(2,307)= 4.785, p= .009). Post hoc LSD tests showed a significant difference between the “No-tapping” and “Tapping” conditions (p< .001 for both tapping with and without noise). There was no difference between the two “Tapping” conditions (p=.215).

When the subitizing range (≤ 3) only was considered, there was a significant effect of the Tapping condition on RTs (F(1,171)= 21.288, p< .001). There was also an effect of Numerosity (F(2,171)= 33.405, p< .001), and a reliable interaction between Numerosity and Tapping condition (F(4,171)= 3.758, p= .006). Post hoc LSD tests showed a significant difference between the “No-tapping” and “Tapping” conditions (p< .001 for both tapping with and without noise). The interaction was due to the effect of numerosity being stronger in the tapping conditions (see Figure 26).

---

[7] The slopes here are expressed in seconds given that RTs were recorded by stopwatch.

For the larger numerosities (5-8), a reliable effect of Tapping condition was found (F(2,172)= 24.243, p< .001). There was a significant effect of Numerosity (F(3,172)= 15.099, p< .001), but no interaction. Post hoc LSD tests showed a significant difference between the "No-tapping" and "Tapping" conditions (p< .001 for both tapping with and without noise). There was no difference between the two "Tapping" conditions (p=.247). RTs were slowed in the tapping conditions, but this did not affect the slope of the function.

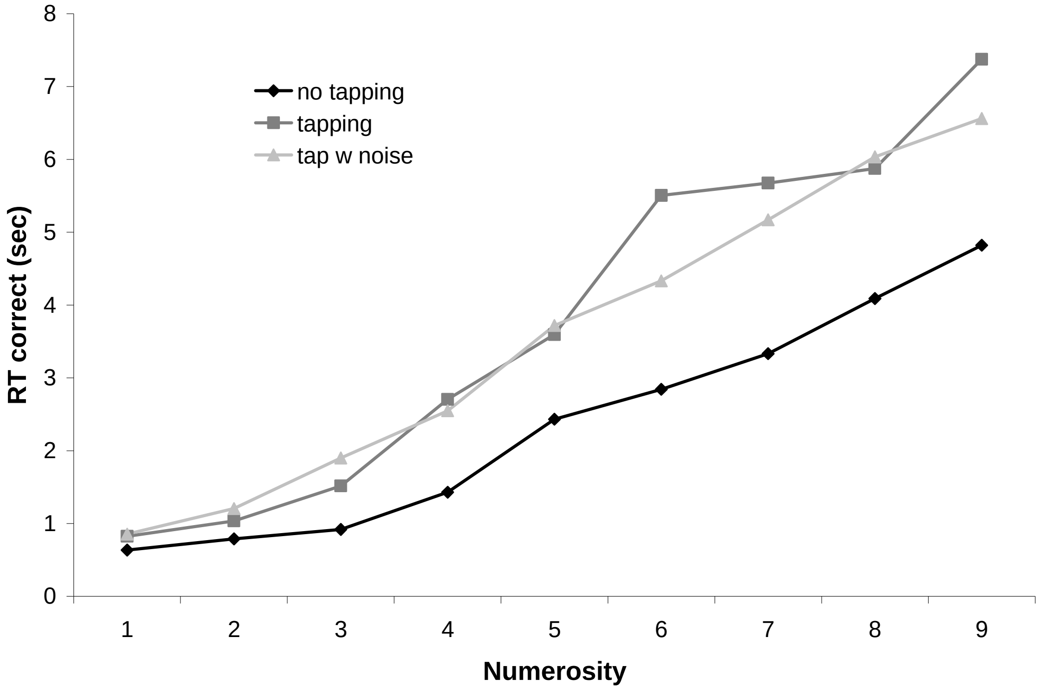


Figure 26. MH's mean correct RTs (s) when correctly enumerating displays of random dots (i) without any tapping, (ii) with tapping each dot and (iii) with tapping each dot while listening to white noise.

Discussion

This experiment again replicates the findings from the previous experiments, where MH demonstrated normal subitizing performance in terms of accuracy (<3 items), in contrast to an impaired counting performance. It was further demonstrated that counting accuracy could be helped by forcing MH to count serially, though the rate of counting remained similar irrespective of whether MH was required to tap. This suggests that MH counted serially in each case, but that having to tap the items helped him keep track of how many items he had found. The generally slower counting, when tapping was required, may simply be due to the extra time needed to make an explicit motor response. On top of this, though, MH showed a larger slope on his subitizing function when he had to tap relative to when he did not. This is consistent with him being able to assimilate subitizable numbers of items in a more parallel manner, faster then serial counting.

Although tapping helped the accuracy of MH’s counting of larger diplays, there was no effect of whether tapping was done with or without white noise. Apparently he did not rely on counting the auditory taps he made. As an alternative I suggest that tapping functioned as a visuo-motor aid, helping MH remember the locations he already visited. Forti and Humphreys (2004) reported a quite similar result in a patient with unilateral visual neglect, where making a pointing response to items significantly improved memory for inspected locations. It appears that the visuo-motor response can provide a substitute spatial representation, when visuo-spatial memory is impaired.

Experiment 3.5: Tests of monitoring

In the final experiment, I examined whether MH’s problems in counting reflected an inability to monitor which items had been checked, rather than an impaired ability to maintain locations that had been visited. It should be noted that MH’s lesion extended into the middle frontal gyrus, and an impairment in controlling selection and in monitoring where attention is allocated may reflect this more anterior damage (Bertelson, 1961; Smith, 1968). To test whether the problem was one of control and monitoring alone, MH performed a search task where he was rewarded (assigned points) for finding successive targets but ‘punished’ (points were removed) if he re-visited a previously selected location which could contain a target.

When each potential target location was selected, he was also asked whether he thought he had visited there before (Bertelson, 1965; Pashler & Baylis, 1991). If there is a problem only in monitoring where search has been carried out, then MH's re-visits of target locations should be no greater than those of controls, but he should be impaired at judging that the locations were re-visited (revealed by a proportional increase in the number of re-visited sites that MH believed he inspected for the first time). On the other hand, an increase in re-visitations, especially re-visitations which occur some time after the initial visit, may reflect impaired visuo-spatial memory (cf. Mandler & Shebo, 1982).

Method

MH was tested along with 6 age-matched control participants (average age was 64.5). Each participant was given a sheet of paper 60cm x 60cm in size, centred at midline. The sheet was marked with 400 dots (each 3 x 3cm apart), and a small thimble was placed over 64 of the locations. Twenty-two targets (small markers) were placed randomly, each under one thimble. The task was to explore all the thimbles to find the targets. For each target found, participants were given a reward of 1 point. For each thimble location re-visited, the participants lost 2 points. Participants were told the rules and instructed not to re-visit a location if they could help it. As each thimble was selected, the target was asked to say whether they were visiting it for the first time or whether they thought they had made an error and were re-visiting it. There were no time limits. The number of detected targets, the number and temporal order of re-visits, and the responses on re-visits were recorded. Each participant took part in 10 trials.

Results

The control participants all detected all the targets. They made on average 5.2 re-visits per search (SD 2.3) and detected that an error had occurred on an average 1.75 (SD 0.8) of these re-visits (detection rate of 33.7%). When new locations were visited, the controls thought that they were re-visiting the location on an average 4.3% of trials. MH detected an average of 91% of the targets. He made an average of 26 re-visits per search task, which was more than 9 SDs from the control mean. All of the re-visits occurred after he had searched at least 3 other potential target locations, suggesting that the re-visits were not due to motor perseveration (see Mannan et al., 2005). On average he reported that he was wrong on 6.5 of the re-visits (detection rate =29.5%). This falls within 2 SDs of the control rate of detecting when a re-visitation occurred incorrectly. When new locations were inspected, MH falsely claimed that a re-visitation was made on 5.4% of the trials.

Discussion

The data from the search task confirm the initial clinical results when MH was asked to perform an invisible star cancellation task – he made frequent re-visits of previously inspected locations. These re-visits typically followed after at least 3 other locations had been inspected, suggesting that re-visits reflected the loss of information about which locations had been searched and not motor perseverations. Despite the abnormal numbers of re-visits, MH made around the same proportions of detection responses as controls (deciding that he had made an error by re-visiting the location). This last result suggests that there was not a marked problem in monitoring, post-selection, when asked to assess whether a location was re-inspected, but there was a problem due to losing information that would otherwise guide him away from inspected locations. MH’s ability to detect re-inspections may be due to residual memories which are too weak to guide search but can raise forced-choice responses to approximately the normal level.

General Discussion

I have presented evidence from a patient, MH, who has impaired spatial memory and who makes abnormally large numbers of re-visitations of inspected locations when visual feedback is minimised in cancellation tasks (see the Case Report). I demonstrated that accuracy in the subitizing portion of the enumeration function was normal while there was dramatic impairment for counting more than 4 elements. MH's performance was greatly improved when the elements were presented in two spatially defined groups, with each group representing a subitizable number. However, colour grouping did not aid MH's performance, despite his being sensitive to colour segmentation (as shown by his improved performance when the two colour groups also form spatial groups; see also Riddoch et al., 2004). It was also shown that MH's counting performance improved when he was forced into a serial mode for enumeration by tapping each dot in sequence. Finally, MH made many re-visitations of inspected locations during search, which is consistent with him having an impaired visuo-spatial memory. However, relative to controls, he did not differ in his ability to detect when re-inspections occurred.

These data support the argument that at least some processes are specific to counting and are not required for subitization – in particular counting but not subitization is dependent on memory for previously inspected locations. Due to MH's impaired visuo-spatial memory, I suggest that he failed to maintain which items had already been inspected and he was unable to count in an efficient serial manner. Counting was aided when the items segmented into two spatial groups because he then had only to maintain the general locations of the groups, and not the locations of the multiple independent stimuli.

One difficulty for the argument that MH had simply lost visuo-spatial memories for stimuli is that his counting performance did improve when he was forced to count serially, by tapping (Experiment 3.4). This can be explained if tapping meant that MH used a separate motor-based memory system, distinct from his impaired visuo-spatial memory, and if his motor memory system is relatively preserved.

An alternative proposal is that there exist different forms of visuo-spatial representation. Some authors (see Lecerf & de Ribaupierre, 2005; and Mammarella et al., 2006) distinguish between two kinds of visuo-spatial memory tasks, each of which requires a memory for patterns of spatial locations, but which differ in the type of spatial process involved: simultaneous in one case (e.g., as measured in pattern memory tests) and sequential in the other (i.e. in the Corsi blocks task). In this framework, MH was impaired at using simultaneously available visuo-spatial memories, but he was able to use sequential visuo-spatial memories – and hence tended to be more accurate when serial processing was encouraged by tapping.

An argument related to this last proposal is that MH is oversensitive to pattern information (there is a form of ‘over-grouping’; see Riddoch et al., 2004). Riddoch et al. had MH search for an orientation-defined target that could sometimes group into a larger visual pattern. MH was markedly impaired when grouping took place. The authors suggested that MH has an over-reliance on visual coding in the ventral stream, and fails to utilise more dorsal visual information in search. When dorsal representations are not used, items tend not to be individuated but are treated instead as an undifferentiated mass, disrupting exact counting (see Humphreys, 1998). With small groups, however, a pattern recognition process could be used, enabling him to ‘subitize’ displays with small numbers of items or displays where the items segment into two small spatial groups. This would fit with the argument that subitizing relies on pattern recognition processes (Mandler & Shebo, 1982; Logan & Zbrodoff, 2003). It would also mesh with the argument that MH is poor at using simultaneously available visuo-spatial memories. According to this account, forcing MH to tap may mean that he ‘weights’ dorsal representations more strongly, leading to better counting.

The impaired visuo-spatial memory and ‘over-grouping’ accounts can make different predictions about the types of counting error that might arise. According to the memory proposal, MH ought to make over-estimations because he should re-visit items/locations that have already been inspected. This would mimic his performance on the hidden cancellation task. In contrast, according to the ‘over-grouping’ account, under-estimations may occur because MH treats items as a group rather than individuating each item. The data here demonstrate a majority of underestimations occurred in each experiment, consistent with predictions of the over-grouping account. It should be noted, however, that the two accounts are not mutually exclusive. MH may tend to group items inappropriately and he may have poor spatial memory for locations he has visited. The fact that MH did make some over-estimations fits with this.

Whichever account is put forward, the data from Experiment 3.5 indicated that the problem was not simply due to poor monitoring of search. When search was measured MH made abnormal numbers of re-visits of inspected locations, but, on forced-choice testing, he could quite often detect that a re-visit occurred. If monitoring was selectively impaired then the number of re-visits should not increase but MH should be impaired at detecting when a re-visitation took place. The results contradict these predictions.

The present results indicate a strong contrast between MH’s performance in the subitization range and with larger magnitudes. At least for displays of up to 3 items, MH showed a normal counting function in terms of accuracy and relatively fast RTS, but both RTs and accuracy deteriorated rapidly for larger magnitudes. There were also differential effects of particular variables on the two parts of the enumeration function. For example, subitization was not affected by grouping or by segmenting the stimuli into colour groups, whereas counting was. In addition, counting was aided by making MH tap items that he counted, whereas subitization slopes tended to increase. The differential effects of these variables is at least consistent with the argument that there is a particular visual process subserving subitization that is spared here, along with an impaired counting function. The data do not differentiate, however, whether subitization is spared due to MH maintaining a preserved number of FINSTs (Trick & Pylyshyn, 1993) or due to him using a pattern recognition process. Further work is required to distinguish these possibilities.

CHAPTER 4:

DIFFERENTIATING SUBITIZING AND COUNTING: A VOXEL BASED CORRELATIONAL STUDY.

Synopsis

The study presented here is the first to assess subitizing and counting in a large sample of neuropsychological patients (34 patients), and to subsequently relate the range of behavioural performances on visual enumeration to a continuous measure of neural integrity using an observer independent voxel-based approach, separating out gray and white matter. Severe impairments in subitizing were associated with damage to the early visual areas and white matter in the occipito-parietal region, even with visual field defects accounted for in the modelling, while later visual areas were associated with less severe subitizing impairments. In contrast, impairments in counting efficiency were associated with damage to a larger fronto-parietal network, including the left angular gyrus as well as higher visual areas. The data support the argument for distinctive processes, and neural areas, supporting subitization and counting.

Introduction

Whether the contrast between efficient enumeration of small number and less efficient enumeration of larger numbers is subserved by separable processes is still under debate. The functional imaging data does not provide a clear picture (see Chapter 1 – functional imaging evidence), in addition, it cannot determine whether the activated areas are necessary for task performance, or simply associated with the task performance. Thus, the key question that remains is whether the structural integrity of the identified regions is necessary for subitizing and/or counting. Complementary data from neuropsychological patient studies is crucial in answering this. Is it possible to dissociate the processes following selective brain lesions?

While there have been numerous case reports of enumeration difficulties in brain-lesioned patients there has been surprisingly little neuropsychological research published on explicit distinctions between subitizing and counting (see Chapter 1 – Neuropsychological Evidence). The previous chapter (Chapter 3) reported a single case, MH, who presented with a striking dissociation in subitizing and counting: MH was still able to subitize (perfect accuracy as well as intact subitizing speed), but demonstrated a marked inability to count larger numbers. This suggests that at least some processes are specific to counting and are not required for subitization.

To date, all the neuropsychological evidence for distinct subitization and counting processes has emphasised behavioural differences between patients, and there is a paucity of data on the underlying neural correlates of any impairments – although distinct correlates of impaired subitization and counting would provide important support for an argument that there are also underlying functional differences. The present chapter provides a first lesion-based analysis of the relations of these different aspects of enumeration. I examined subitization and counting across a case series of brain lesioned patients with chronic deficits, correlating any behavioural deficits with data from whole-brain analyses of high resolution MRI scans. To derive single measures of either subitization or counting, an efficiency measure (RT/proportion correct; Townsend & Ashby, 1983) was used that enabled the inclusion of patients with severe difficulties. (where performance accuracy would normally be reported, cf. Dehaene & Cohen, 1994) and those with relatively mild deficits (where the slopes for subitization and counting latencies are more typically analysed: e.g. Lemer, Dehaene, Spelke, & Cohen, 2003; Ashkenazi, Henik, Ifergane, & Shelef, 2008; Halpern, Clark, Moore, Cross, & Grossman, 2007). Previously patients with severe and mild impairments have been considered separately.

The study presented here is the first to assess subitizing and counting in a large sample of brain-damaged patients (34 patients), and to subsequently relate the range of behavioural performances on visual enumeration to a continuous measure of neural integrity. Patients were not selected on the basis of their enumeration performance and had been referred to the Birmingham Univeristy Imaging Centre for a variety of reasons. All patients were prospectively scanned with a high resolution MRI scan, and an observer independent voxel-based correlational method (similar to studies by Tyler et al., 2005; Acres, Taylor, Moss, Stamatakis, & Tyler, 2009) was used to test for correlation between performances and tissue abnormality across the whole brain. This avoids biasing the results to any a-priori pre-specified region. Equally, patients were not selected on the basis of their behavioural performance, thereby allowing for a large range of performances, from unimpaired, through to severe impairments. By including all these patients in the analysis, again bias is removed and the power of the findings increases. This is because these patients with good performance act as very strong control participants for more general cognitive impairments, in so far that their brain lesions are not crucial for subitizing and/or counting.

By assessing behaviour for both the subitizing and counting range in our patients, we aimed to identify the underlying brain regions necessary for these two aspects of enumeration.

Method

Participants

All the patients participating in this study were recruited from the long-term panel of neuropsychological volunteers established by the Behavioural Brain Sciences Group and the Birmingham University Cognitive Screen (BUCS, www.bucs.bham.ac.uk) at the School of Psychology, University of Birmingham. The only inclusion criteria when recruiting participants were that (a) the patients had acquired brain damage (various etiologies, e.g. stroke, carbon monoxide poisoning, degenerative) and were not in an acute stage (> 9 months post injury), and (b) the patient had a T1 weighted 3T MRI scan. Thirty-four brain injury patients agreed to participate. The age of patients (27 males and 7 females) ranged from 36 to 86 years (mean age 65 years). To establish the range of performance with the healthy population, eight (1 female, average age 65 years) age-matched control participants were also included in the study. Each participant provided informed consent according to the procedures in agreement with ethics protocols at the School of Psychology and Birmingham University Imaging Centre (BUIC). More details about the patients are provided in the Supplementary Table 1.

Cognitive assessment

The experiment was programmed and run using E-prime 1.1 software (Schneider, Eschman, & Zuccolotto, 2002). The displays were presented on a black background on a 17 inch monitor with 1024x768 pixel screen resolution. Each participant was positioned approximately 65 cm from the screen. The stimuli consisted of 1 to 9 grey dots (RGB: 190,190,190), which were drawn randomly within the centre 500x500 pixels of the screen (14.4 ° visual angle). The dots had a diameter of 25 pixels (1.4 ° visual angle) and any two dots were separated from each other by a minimum distance of one dot diameter.

One trial started with the presentation of a fixation cross in the centre of the screen for a duration of 1000ms. Next, the enumeration display appeared and remained on the screen for an unlimited duration until a response was made. Participants were instructed to enumerate the dots in this display as accurately and quickly as possible. As soon as they felt they knew the correct response, they had to press the space bar and simultaneously spoke their response. When the spacebar was hit, the dot display disappeared and was followed by a blank screen, where the experimenter entered the reported number using the numeric key pad (for a similar method, see Atkinson et al., 1976; Watson & Humphreys, 1999; Watson & Maylor, 2006). Accuracy and reaction times were recorded.

All participants completed 6 blocks, with each block containing 45 randomly ordered trials (5 per numerosity). This resulted in a total of 30 trials per numerosity (1-9).

Voxel-based correlation analyses

Patients were scanned at BUIC on a 3T Philips Achieva MRI system with 8-channel phased array SENSE head coil. The standard anatomical scan was acquired using a sagittal T1-

weighted sequence (sagittal orientation, TE/TR=3.8/8.4ms, voxel size 1x1x1mm, scanning time approximately 5 minutes).

Image pre-processing.

All T1 scans were transformed into the standard MNI space using SPM5 (Statistical Parametric Mapping, Welcome Department of Cognitive Neurology, London UK). Although earlier versions of SPM struggled with segmenting brains containing large lesions (e.g. Tyler & Stamatakis, 2005), we applied the advanced unified-segment procedure as implemented in SPM5 (Ashburner & Friston, 2005). This procedure has been shown to be optimal for spatial normalization of lesioned brains (Crinion et al., 2007). Briefly, the unified-segmentation procedures involve tissue classification based on the signal intensity in each voxel as well as on a-priori knowledge of the expected localization of grey matter (GM), white matter (WM), cerebrospinal fluid (CSF) in the brain, along with an extra class which is included to account for other sources of signal variability. The procedures are applied to iteratively segment the tissues and warp them onto standard space (Ashburner & Friston, 2005). The procedure results in 3 classified tissue maps which indicate the probability that a given voxel 'belongs' to a specific type of tissue: gray matter (GM), white matter (WM) or cerebro-spinal fluid (CSF) (see Figure 27). Given that we tested only chronic patients, the region of the damaged tissue was replaced by CSF in the majority of cases (Higgs et al.,2008), In addition, to ensure that abnormal GM/WM tissue intensities were not classified as normal, the number of Gaussians per class was restricted to 1 for both GM and WM.

We visually inspected each of the segmented images to assess whether the segmentation and normalisation procedures were successful. Figure 27 provides an example of the segmented images for 2 patients, along with the normalized whole brain image for each case. Finally, the segmented images were smoothed with a 12-mm FWHM Gaussian filter to accommodate the assumption of the random field theory used in the statistical analysis (Worsley, 2003). The pre-processed T1 scans, the grey and the white matter maps were then used in the analyses carried out to determine voxel-by voxel the relationship between brain damage and our measures of visual enumeration (see below).

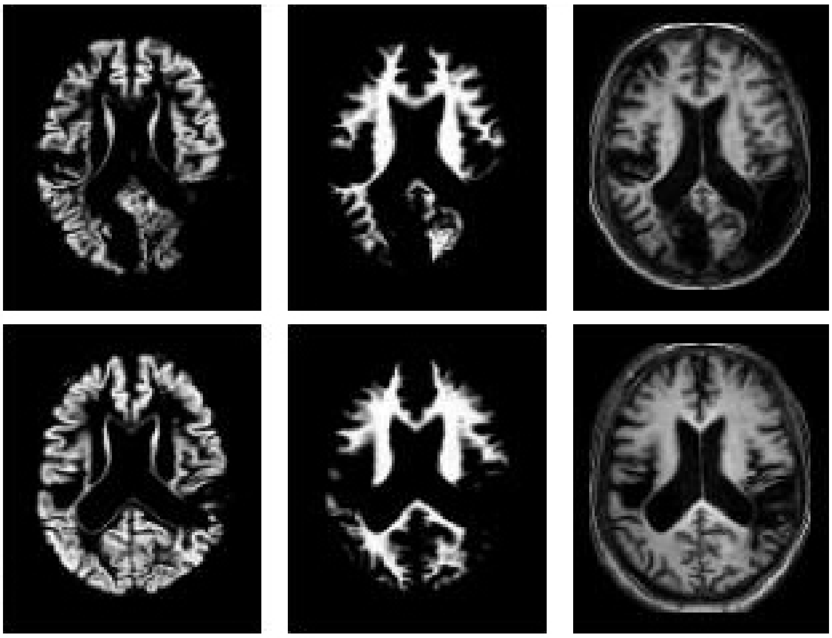


Figure 27. Examples of segmented grey matter for 2 of the patients in the study, from left to right: grey matter maps, white matter maps and a normalized T1.

Voxel-based morphometry.

Scans from 34 patients, segmented into individual white matter and grey matter maps (see above for the pre-processing protocol), were used in the statistical analysis with SPM5. The voxel-by-voxel correlational relationship between the behavioural measures of visual enumeration and the damaged tissue was assessed separately for grey and white matter integrity. The patients were separately divided into five groups ranging from no impairment to a severe impairment for (i) subitizing (the slope of the efficiency function across displays with

2-4 items), and (ii) counting (the slope of the efficiency function across displays with 5-8 items). The highest (9) and lowest numerosities (1) were left out of the analysis due to possible guessing "end-effects" (see Trick & Pylyshyn, 1994). The 5 groups were determined based around the average control performance as well as the average patient performance. Patients who performed better than the average of the patients and either around or slightly less than the control means were assigned to three groups from mild to non-impaired. Patients who preformed worse than both the patient mean and the controls were classified as severely or moderately impaired. The non-impaired patients (group 0) fell within 3 standard deviations (SDs) of the control mean; moderately impaired patients (group 1) fell 3 to 6 SDs below the control mean; the mildly impaired patients fell 6 SDs or more from the control mean and were better than the patients' average (group 2). The more impaired patient groups were defined according to whether (i) they fell no more than 3SDs below the average across the patients (moderately impaired, group 3) or (ii) they fell more than 3SDSs from the average across the patients (severely impaired, group 4).

We used a full factorial model with one factor (level of impairment) containing 5 cells, in the framework of the general linear model (Kiebel & Holmes, 2003). A separate model was created for the subitizing and counting tasks. However to account for potential co-variation effects in the statistical models, we used performance in the other range as a covariate in the analysis for subitizing and for counting (i.e., using counting and subitization performance respectively as covariates). Additionally, in the statistical model, we added a binary covariate for the presence of a visual field deficit, so that any results cannot simply be explained by patients simply not seeing (part of) the display. We also added a binary covariate detailing whether the patient had any attentional deficit (neglect or extinction, classified using cancellation measures taken from the BUCS; www.bucs.bham.ac.uk) in order to rule out that errors in subitizing or counting were simply due to impairments in attention to one side of the display. Finally we also included, as covariates of no interest, type of brain damage, age, handedness and gender (see Supplementary Table 1 for an overview of the covariates for individual patients). We tested for regions that showed a decrease in GM/WM with decrease in subitization or counting performance. To do this we used the following contrast,across the 5 levels of performance level from non-impaired to severely impaired : [2(non-impaired) 1(slight impairment) 0(mild impairment) -1(moderate impaired) -2(severely impaired)]. The results are reported based on a combination of effect size and cluster size. Clusters larger than 60 mm^3 (i.e. 30 voxels) in which all voxels showed a reliable effect at $p<0.001$ uncorrected were considered reliable. The anatomical localization of the lesion sites was based on the Duvernoy Human Brain Atlas (Duvernoy, 1991), the white matter pathways were identified using the MRI Atlas of Human White Matter by Mori et al. (2005) and brain coordinates throughout are presented in the standardized MNI space.

Results

Behavioural Results

Patients were classified based on the slope of the efficiency function in the subitization and counting ranges. In one case a patient had a negative slope (i.e., increasing efficiency as the display size increased) due to extremely poor performance when small numbers were enumerated. In one other case, a patient did not have a single accurate response in the counting part of the function. In both instances, patients were assigned to the maximally impaired group for that range of enumeration.

Subitizing

For the subitizing range (2 – 4 items), the patients' accuracy scores ranged from 37% to 100% correct, with an average of 93.54 (SD= 12.77). The controls average was 99.9% (SD= 0.3). Efficiency (RT/prop. corrrect) slopes of correct responses were calculated for all patients and controls. The subitizing slopes for the patients ranged from 26.7 to 7056.9 (ms/prop. correct), with an average of 994 (SD=1662.9). The slope for the controls was on average 95.9 ms/prop. correct (SD=27.6).

The patients were assigned to a subitizing impairment level group based on these efficiency slope measures. A full overview of this assignment can be found in Supplementary Table 1. The range of values for each group is depicted in Figure 28[8].

Figure 28. The range of efficiency slope values for each group of patients. Patients were assigned to different levels of subitizing impairment based on their performance compared to controls and compared to the overall patient group. The numbers of patients per groups was 8, 3, 16, 5 and 2 respectively for the unimpaired, slight, mild, moderate and severe impairment groups.

---

[8] Note that the Y axis is converted to a logarithmic scale here to allow for the large range of values to be represented.

Counting

The healthy controls had an average of 98.4% correct (SD= 1.3). The slopes of efficiency across display sizes 5-8 for the patients ranged from 199.2 to 125370 ms/prop. correct with an average of 13009 (SD=32376). The controls' average was 267.8 ms/prop. Correct (SD=116.5). The patients were assigned to a counting impairment level group based on these efficiency slope measures. A full overview of this assignment can be found in Supplementary Table 1. The range of values for each group is depicted in Figure 29.

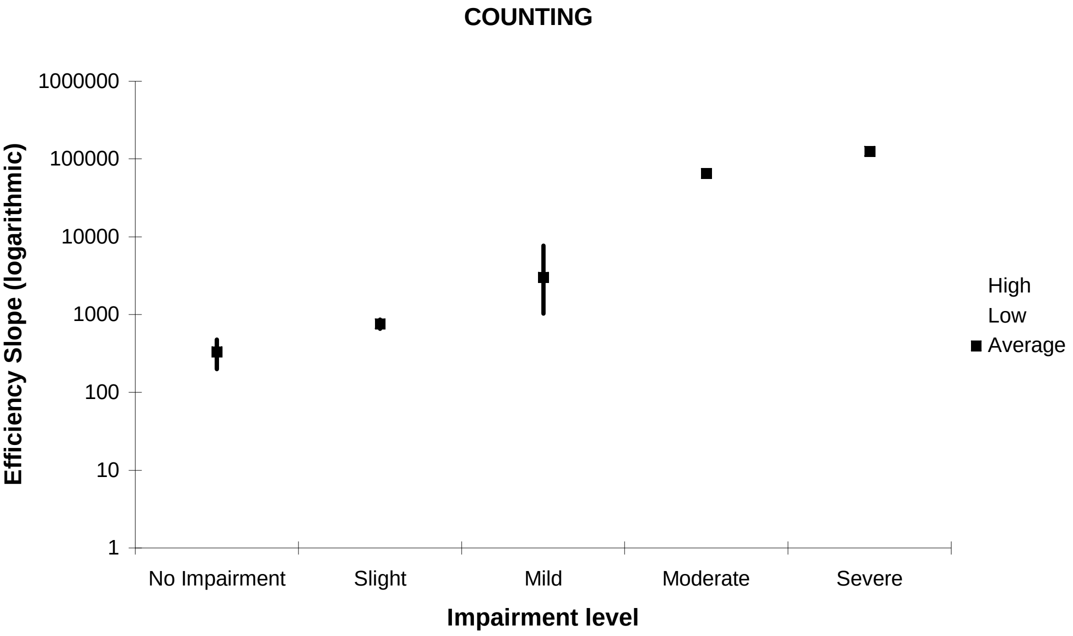


Figure 29. The range of efficiency slope values per group of patients. Patients were assigned to different levels of counting impairment based on their performance compared to the controls and to the overall patient group. The number of patients in each group was 7, 5, 18, 2 and 2 respectively for the unimpaired, slight, mild, moderate and severely impaired groups.

Imaging Results

We used Voxel-based morphometry based on general linear model statistics to test subitizing and counting specific impairments in relation to tissue abnormality in the patients. The analysis demonstrated a marked dissociation between the neuroanatomical substrates of subitizing and counting performance.

Subitizing

Grey Matter. For subitizing, we found that several foci in the right occipital cortex showed reduced grey matter with increases severity in subitizing (Figure 30, Table 2): right precuneus, right middle occipital gyrus; and right lateral occipital sulcus. In addition changes in GM in the left calcarine gyrus and left basal ganglia were also associated with increasing levels of impairment in subitizing. It is worth noting that the evidence for reduced GM in the left calcarine region (see Figure 30, plot a) was only apparent in the group categorised with a severe impairment in subitizing. This might reflect the presence of a right visual field deficit in that group. However, against this, the majority of patients (8/10) who had visual field deficits were not even moderately impaired in subitizing (see supplementary Table 1 for details). Also the presence of a field deficit was included as a covariate in our model, so this may not be a critical factor. Other covariates in our model were counting performance, attentional deficits, and age. The analysis indicates that these factors were not responsible for the effects of brain lesion on subitization.

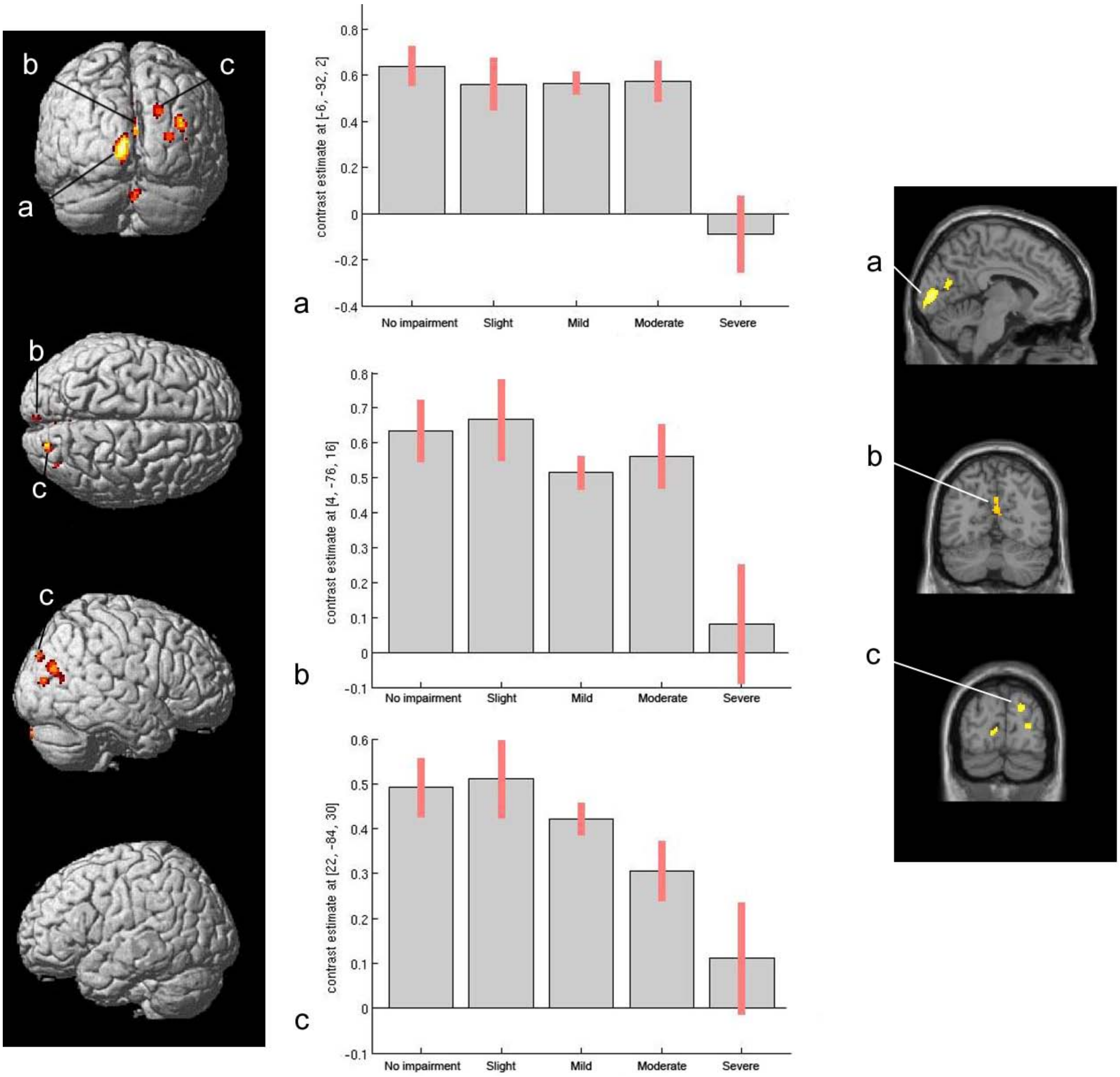


Figure 30. Brain regions corresponding with a decrease in Grey matter associated with a gradually increasing impairment in subitizing. Graphs depict contrast estimates and 90% confidence intervals for the different subitizing groups in a) calcarine sulcus, b) precuneus and c) lateral occipital sulcus

White Matter. The same analysis and contrast was performed with the segmented and smoothed white matter (WM) maps. Increasing impairments in subitizing were associated with reduced WM in part of the corona radiata in the vicinity of the parieto-occipital sulcus (Table 2). This deficit in white matter suggests that parieto-occipital disconnection is detrimental to accurate and efficient subitizing performance.

Finally, to ensure our results were not caused by artefacts when the segmentation procedure was applied to large brain lesions, we carried out a whole brain analysis, where we simply used the smoothed (10mm Gausian) normalised T1 scans for the patients (using an identical method to Acres et al., 2009; Tyler et al., 2004; Stamatakis & Tyler, 2005). Similar to the results reported above this analysis revealed that changes in 2 large clusters within the occipital cortex were associated with gradual impairments in subitizing. These clusters overlapped with the occipital areas that revealed in the analysis of the segmented tissue maps: the left calcarine gyrus and the right middle occipital gyrus. These results are reported in the supplementary material (Supplementary Table 2 and Figure 1).

Table 2. Summary of a random effects analysis linear decrease contrast for the 5 subitizing groups. The results reflect voxel-based correlations of voxel signal intensities across the entire brains of 34 patients. X, Y, and Z refer to the stereotaxic MNI coordinates of the peak of the cluster. The threshold for significance of the clusters reported here was set at a voxel-wise uncorrected p< .001 – whole brain - and a spatial extent of 30 voxels. The underlined areas denote the regions for the regions presented in Figure 30.

Cluster size	*Z*	*X*	*Y*	*Z*	*Location*
Grey Matter					
193	3.43*	4	-76	16	R Precuneus
36	3.65	22	-84	30	R Lateral Occipital sulcus
32	3.51	28	-82	12	R Lateral Occipital gyrus
84	3.38	36	-72	24	R Middle Occipital gyrus
210	4.40*	-24	-14	22	L Basal Ganglia
197	4.18*	-6	-92	2	L Calcarine sulcus
40	3.99	2	-90	32	R Cerebellum
White Matter					
54	3.70	20	-66	38	R Corona Radiata

* cluster significant at whole brain corrected .05 level

Counting

Grey Matter. For counting, we found that damage to GM in left fronto-parietal regions was associated with the severity of impairments (Figure 31, Table 3). Specifically, GM reduction was linked to poor counting in the following frontal regions: left frontopolar, superior frontal and lateral orbital gyri; it was also associated with impaired counting in the following occipito-parietal regions: the left angular gyrus, the parieto-occipital fissure, the left middle occipital gyrus,and the left superior calcarine area. These results emerged with covariates included for attention deficits, subitizing performance, visual field deficits and age of patient.

It is interesting to note that even a relatively mild drop in GM integrity in the angular gyrus led to some impairment in counting performance (Figure 31, plot a), with larger behavioural impairments associated with even larger losses in GM in this region. Both the moderate and the severely impaired groups showed a more degraded loss of GM in this region linked to poor counting, compared with the mild and slightly impaired group. However the moderately impaired patients, if anything, showed slightly greater GM loss than the severely impaired group. This pattern is difficult to account for, though we note that the specific contrast between moderate and severe impairments is based on small patient numbers (2 severe and 2 moderate).

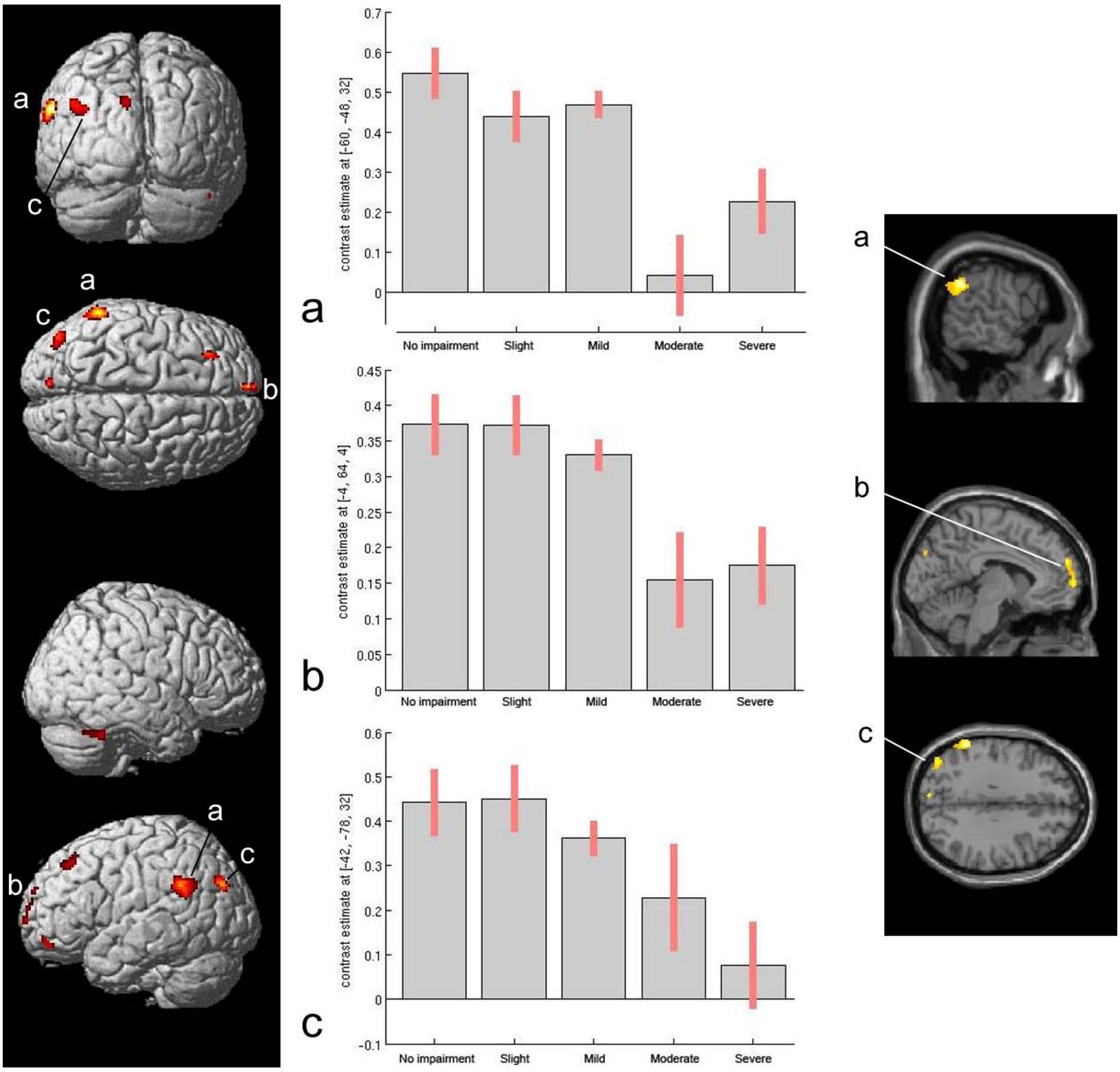


Figure 31. Brain regions where decreases in Grey matter were associated with increasing impairments in counting. Graphs depict contrast estimates and 90% confidence intervals for the different subitizing groups in a) L angular gyrus, b) L frontopolar gyrus and c) L middle occipital gyrus.

White Matter. The same analysis was performed with the segmented and smoothed WM maps. The white matter regions that were significantly associated with increasing impairments in counting are given in Table 3. The most notable association was between impaired counting and changes to the corona radiata leading to the left middle frontal gyrus.

This suggests that a fronto-parietal disconnection is detrimental to an accurate and efficient counting performance.

Table 3. Summary of a random effects analysis linear decrease contrast for the 5 counting groups. The results reflect voxel-based correlations of behaviour with signal intensities across the entire brains of 34 patients. The X, Y, and Z values refer to the stereotaxic MNI coordinates of the peak of the cluster. The threshold for significance of the clusters was set at a voxel-wise uncorrected p< .001 – whole brain - and a spatial extent of 30 voxels. The underlined areas denote the regions presented in Figure 31.

clustersize	*Z*	*X*	*Y*	*Z*	*Location*
Grey Matter					
183	4.43*	-60	-48	32	<u>L Angular gyrus</u>
87	4.09	-4	64	4	<u>L Frontopolar gyrus</u>
30	3.83	-8	-86	34	L Parieto – occipital fissure
80	3.71	-42	-78	32	<u>L Middle Occipital Gyrus</u>
37	3.65	-42	50	-14	L Lateral Orbital gyrus
58	3.59	-22	-54	16	L Anterior Calcarine gyrus
48	3.58	-30	32	46	L Superior Frontal gyrus
47	3.43	48	-48	-32	R Cerebellum
White Matter					
66	3.74	34	-52	-38	R Middle Cerebellar peduncle
44	3.73	12	54	16	R Corona Radiata
171	3.68	-36	18	48	L Corona Radiata

* cluster significant at whole brain corrected .05 level

Discussion

This chapter presents the first ever lesion-symptom analysis of deficits in enumeration after brain lesion. Here, the slopes of the function for the efficiency of enumeration were examined, integrating measures of response speed and accuracy in the subitizing (2-4) and counting range (5-8). The data point to a clear dissociation between the sites of damage associated with selective problems in subitizing (extracting out variance associated with impaired counting) and with selective problems in counting (extracting out variance associated with subitizing). Impaired subitizing was linked to damage in a number of occipital and parietal regions bilaterally, including the left calcarine gyrus, middle occipital gyrus and lateral occipital sulcus as well as the right precuneus. There were also associated changes in the left basal ganglia. There was also white matter change in the vicinity of the right parieto-occipital sulcus. In contrast, impairments in counting were linked to damage in several regions in parietal-frontal cortex including the left angular gyrus, the middle occipital gyrus, the superior frontal gyrus and left fronto-polar regions. The correlations of the neural changes with deficits in enumeration occurred even with variance due to the presence of visual field defects and attentional problems (e.g., neglect) factored out.

It is an obsolete point to ask whether the severely impaired patients who cannot reliably enumerate even as few as 2 objects (when accuracy is considered) can count larger numerosities, they cannot. However, the groups reflect differences in the relative severity of impairments compared to the other patients in the sample, separately for subitizing and counting. For example, in relation to the other patients, patient 2 is very severely impaired at subitizing, yet still manages to get some numerosities in the counting range correct (10% accuracy, probably due to estimating, see Demeyere & Humphreys 2007), patient 7 on the other hand has only a mild impairment in subitizing, but is extremely poor at counting, this is similar to the patient reported in Chapter 3.

Subitizing

The evidence for changes to visual processing regions and the precuneus in relation to impaired subitization fits with the proposal that subitization depends on the efficient, parallel apprehension of a small number of objects. When areas critically involved in this parallel apprehension process are damaged, and/or when there is disconnection of these regions (especially in the right hemisphere; see WM result), then subitization breaks down. The areas of damage associated with poor subitization here are associated with simultanagnosia (e.g., Riddoch et al., in press), and we might expect that a lesion that impairs the rapid apprehension of a small number of objects will lead to patients being aware only of a limited number of objects at a time.

Other studies have also found simultanagnosia to be linked to poor subitizing ability (Dehaene & Cohen, 1994; Humphreys, 1998; Demeyere & Humphreys, 2007) as well as to a poor representation of the 'whole' (e.g. Coslett & Saffran, 1991; Friedmanhill et al., 1995). It is therefore conceivable that similar mechanisms underly both detailed global perception and subitizing.

Himmelbach et al. (2009), in an event related fMRI study of a simultanagnosic patient, found bilateral activations for the primary intermediate sulcus and the precuneus when the patient has correctly seen 'the whole' global stimulus, compared to when she was not able to see the global level. It can be argued that this awareness of the whole is impaired in patients with simultanagnosia, and that despite their ability to attend to scenes in a distributed mode of attention (e.g. see Demeyere & Humphreys, 2007), the global processing is unconscious and approximate. The precuneus is here again found to be a crucial structure for the ability to subitize (Himmelbach, Erb, Klockgether, Moskau, & Karnath, 2009).

Xu and Chun (2006; 2009) have recently argued from fMRI data with normal observers that a region around the inferior intra-parietal sulcus responds to the presence of a maximum of about 4 individuation objects in visual short-term memory tasks. The damaged white matter in part of the corona radiata in the vicinity of the parieto-occipital sulcus fits with a disconnection account linking the precuneus to the inferior intra-parietal sulcus poor subitizing and might be critical for transmitting visual input into a visual short-term memory in the intra-parietal sulcus.

Others (e.g. Duncan et al., 2003) have argued that simultanagnosia is linked to slowing of information processing speed when measured within the framework of the theory of visual attention (Bundesen, 1990), but not impaired VSTM itself. This slowing of visual processing speed could link to the white matter disconnection, while damage to the inferior IPS itself is not selectively associated with poor subitization.

Counting

In previous fMRI studies on counting, Piazza et al. (2003) found a large network of bilateral occipital, parietal, insular, prefrontal and subcortical areas to be more activated for enumerating 4 to 7 elements compared to 1 to 3 elements. This matches our data in that we as well find a network of higher occipital, parietal and frontal areas although it is more lateralized to the left. This may mean that although bilateral activation is found in fMRI, only the left areas are critically necessary for the ability to count.

Ansari and colleagues (Ansari, Lyons, van Eitneren, & Xu, 2007) found greater activation for large than small numerosities (in a comparison task rather than visual numeration) in the calcarine and the parieto-occipital sulcus. This fits with part of our results where we find the parieto-occipital fissure to be critically involved in increasing impairments in counting larger numerosities (5-8).

The left angular gyrus features prominently in our counting results. This matches fMRI results from more abstract number processing, where the angular gyrus is associated with calculation and the retrieval of arithmetic facts (e.g. Grabner et al., 2009). The neuropsychological syndrome associated with problems in more general number understanding and mental calculation is dyscalculia, and this has notably been associated with lesions to the left angular gyrus. Damage to the angular gryus is also linked to Gerstmann's syndrome, where acquired dyscalculia co-occurs with finger agnosia, left-right disorientation and agraphia (Gerstmann, 1940). The left angular gyrus has additionally been found to be more strongly activated during exact compared to approximate arithmetic (Dehaene, Spelke, Pinel, Stanescu, & Tsivkin, 1999). The findings from this VBM study, that damage to the left angular gyrus predicts difficulties specifically in counting, fits with this.

Recent neuro-imaging evidence for the four domains underlying Gerstmann's syndrome found there was no overlap of cortical activation patterns for the four domains in single subject analysis, however DTI analysis revealed the activations all connected to a shared white matter region in the inferior part of the left angular gyrus (Rusconi et al., 2009), the same subcortical region of the focal ischaemic lesion in the most recent case study of pure Gerstmann syndrome (Mayer et al., 1999). Changes to white matter in the vicinity of the angular gyrus were also noted here.

Finally, the more frontal-parietal WM disconnection we found may be linked to areas related to working memory and visuospatial attention as well as saccadic behaviour (e.g. Postle, Berger, Taich, & D'Esposito, 2000).

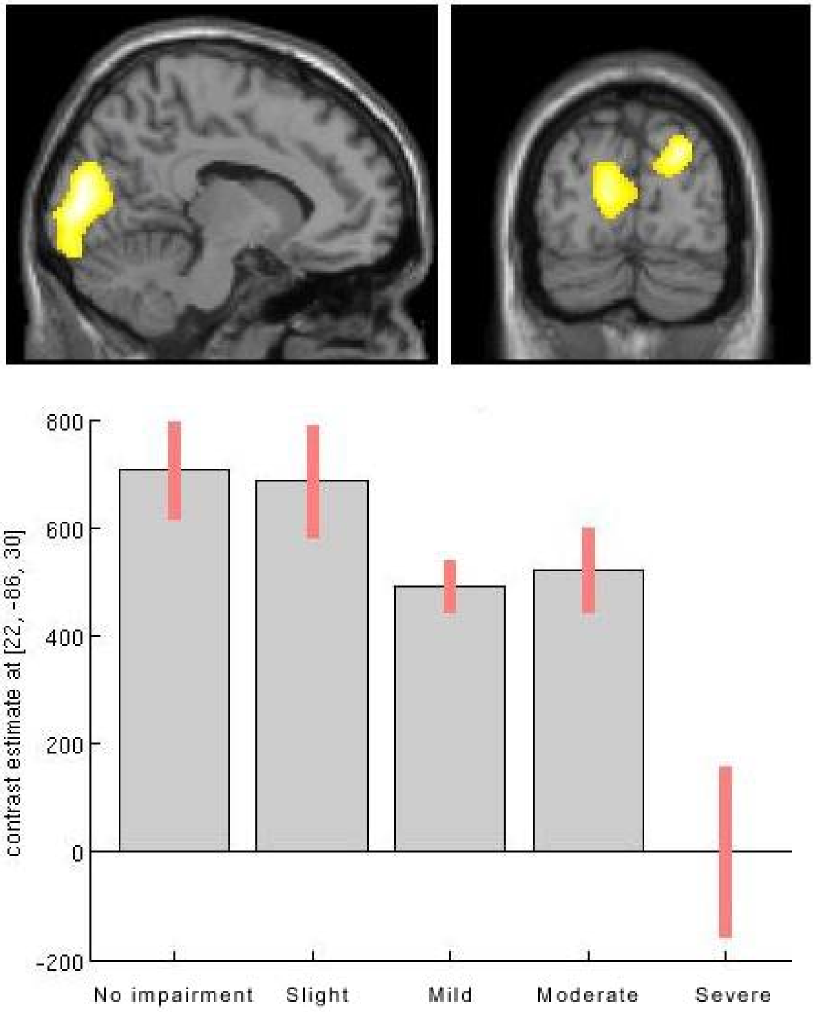
In summary, in accordance with fMRI data, it seems that subitizing and counting can be separated on a neuro-anatomical basis. Here, for the first time, we have demonstrated the necessary regions associated with different levels of impairment in subitizing and counting by using a voxel-by-voxel correlation method, in a large sample of neuropsychological patients. Importantly, we were able to separate out grey matter and white matter damage. For subitizing, a more severe impairment is associated by damage to the early visual areas and precuneus, and is related to patients with the clinical disorder of simultanagnosia. The areas match those found in fMRI studies of subitizing and are in line with theories of a capacity limited VSTM as well as global perception.

Conclusions

In sum, counting impairments are associated with damage to a large fronto-parietal network, including the left angular gyrus, and higher visual areas. This matches fMRI activations in counting tasks (Sathian et al., 1999; Piazza, Giacomini, Le Bihan, & Dehaene, 2003). The angular gyrus damage may disrupt the ability assimilate exact number, critical not only to counting but also to general numerical cognition.The damage to more frontal regions, associated with poor counting, may reflect additional processes such as keeping a running count of the items and guiding visual attention. In contrast, poor subitization was linked to damage to earlier visual areas and to white matter underlying the occipito-parietal region. The data highlight that deficits to the enumeration of small and larger numbers follow different lesions, supporting the argument for the functional distinction between subitization and counting.

Supplementary Table 1. Patient number with corresponding covariates and impairment groups

Patient	VIS FIELD	ATTENTION	STROKE	Gender	Age	Handedness	SUBacc	SUBeffslope	Level	CNTacc	CNTeffslope	Level
1	1	1	0	1	64	Right	36.67	**7056.934**	**4**	0	125370.3	**4**
2	1	1	1	1	63	Right	65.00	7056.934	**4**	10	60281	**3**
3	0	0	0	1	40	Right	81.67	893.751	**2**	43.3	3986.097	**2**
4	1	1	0	2	66	Right	72.50	2409.722	**3**	7.5	70860	**3**
5	1	1	1	1	60	Left	84.16	730.47	**2**	38.33	5862.314	**2**
6	1	0	1	2	64	Left	89.16	2463.168	**3**	63.33	6509.231	**2**
7	0	1	1	1	67	Left	90.00	572.412	**2**	42.5	125370.3	**4**
8	1	0	1	1	72	Right	91.67	**167.952**	**0**	84.16	475.405	**0**
9	1	1	1	1	74	Right	95.83	291.819	**2**	84.16	1680.014	**2**
10	0	0	1	2	82	Right	93.33	1797.896	**3**	60.83	4290.151	**2**
11	0	1	1	1	74	Left	98.33	248.574	**1**	85	772.006	**1**
12	0	0	1	1	76	Right	95.83	142.599	**0**	85.83	1968.495	**2**
13	0	0	1	1	67	Right	99.17	159.791	**0**	96.67	442.127	**0**
14	0	1	1	1	53	Right	99.17	359.313	**2**	89.17	821.894	**1**
15	0	0	0	1	71	Right	97.50	767.162	**2**	90.83	1250.934	**2**
16	0	0	0	1	54	Right	99.16	110.305	**0**	94.17	656.063	**1**
17	0	0	1	1	77	Right	100.00	168.936	**0**	98.3	199.163	**0**
18	0	0	1	1	62	Right	100.00	92.226	**0**	97.5	238.678	**0**
19	0	0	0	1	55	Right	100.00	26.724	**0**	100	212.215	**0**
20	0	1	1	2	60	Right	100.00	67.96	**0**	100	456.247	**0**
21	0	0	1	1	36	Right	99.17	219.988	**1**	91.67	1277.729	**2**
22	0	0	1	1	73	Right	100.00	209.794	**1**	99.17	859.784	**1**
23	0	0	1	1	74	Right	99.16	411.632	**2**	95	2105.651	**2**
24	0	0	1	1	86	Right	99.16	276.401	**2**	90.83	1065.091	**2**
25	0	1	1	2	72	Right	100.00	632.569	**2**	98.33	1030.522	**2**
26	0	0	1	1	62	Right	100.00	314.517	**2**	88.33	1132.787	**2**
27	0	1	0	1	53	Right	100.00	638.034	**2**	44.17	7660.164	**2**
28	0	1	1	2	60	Right	98.30	559.349	**2**	70	1065.627	**2**
29	0	0	1	1	73	Right	98.28	667.263	**2**	78.96	2864.471	**2**
30	0	0	1	2	60	Right	100.00	506.567	**2**	85	1763.95	**2**
31	0	1	1	1	64	Right	100.00	538.783	**2**	100	313.822	**0**
32	1	1	1	1	77	Right	99.17	287.314	**2**	91.67	714.508	**1**
33	0	0	0	1	62	Right	97.50	997.094	**3**	61.67	1816.12	**2**
34	0	0	1	1	48	Right	100.00	1976.514	**3**	100	6963.526	**2**



Supplementary Figure 1
Brain regions associated with increasing impairments in subtizing from whole brain analysis. The graph depicts contrast estimates and 90% confidence intervals for the different subitizing groups in R lateral occipital cortex

Supplementary Table 2. Summary of a random effects analysis linear decrease contrast for the 5 subitizing groups. The results reflect voxel-based correlations of behaviour with signal intensities across the entire brains of 34 patients. The X, Y, and Z values refer to the stereotaxic MNI coordinates of the peak of the cluster. The threshold for significance of the clusters was set at a voxel-wise uncorrected p< .001 – whole brain - and a spatial extent of 30 voxels.

clustersize	*Z*	*X*	*Y*	*Z*	*Location*
Whole Brain					
1512	4.50*	-10	-90	8	L Medial Occipital cortex
962	4.35*	22	-86	22	R Lateral Occipital cortex

*cluster significant at whole brain corrected .05 level

CHAPTER 5:

AUTOMATIC SMALL NUMBER PERCEPTION THROUGH DIRECT SUBITIZATION.

Synopsis

Evidence is presented for the automatic apprehension of exact small quantities, independent of pattern recognition, based on carry-over effects between magnitudes in a quantification task (are the number of items greater or smaller than?). Four serial reaction time studies are reported examining performance across consecutive trials in which numbers were assigned to the same response category (both smaller or both larger than the comparison number). In every experiment ‘same’ response reaction times were slowed when consecutive trials contained small numbers that differed in quantity compared with when there were either repeats of the same exact pattern or repeats of the same quantity. This contrasted with performance on the larger quantities, where performance did not differ across conditions in which there were repeats of the same exact quantity, or different quantities belonging to the same response category. The effects with larger numbers were affected by visual similarity, based on whether similar proportions of items in the display had the same contrast polarity, while effects of repeating the same small quantity were unaffected by this. The data cannot be explained in terms of simple visual similarity, changes in surface area, luminosity changes, changes in visual discriminability or differences in response categories between small and large numbers. Instead, the reduced repetition effects for small numbers differing in quantity suggest that small exact quantities are recognised automatically through direct subitization.

This chapter has been submitted to *Journal of Experimental Psychology: Human Perception and Performance.*

Introduction

Traditionally, the issue of whether there is a special process that underlies subitization, distinct from both pattern recognition and estimating, has been researched using direct measures of enumeration speed and accuracy, but this has not led to an unequivocal conclusion. The present chapter takes a different approach and investigates the properties of subitizable magnitudes indirectly by examining carry-over effects in a serial quantification task (are the number of items greater or smaller than a given target number?).

In serial reaction time (SRT) tasks participants respond faster and more accurately if they have to repeat the response from the previous trial, provided the interval between the last response and the appearance of the next stimulus is reasonably short (Bertelson, 1961; Smith, 1968). This speeded response could be due to a faster identification of the second stimulus, faster response selection or a faster response execution, or any combination of these processes in the S-R chain. The Information Reduction Paradigm (IRP) separates the different contributions of stimulus- and response-related processing by distinguishing between identical, equivalent and different stimulus-response transitions (Bertelson, 1965; Pashler & Baylis, 1991). Identical transitions are when both the stimulus and the response are repeated on two subsequent trials; equivalent transitions occur if only the response is repeated, and different transitions if neither the stimulus nor the response is repeated from one trial to the next. The IRP has been applied in different studies that have shown that the repetition effect can be due to a faster S-R translation (Rabbitt, 1968; Pashler & Baylis, 1991; Campbell & Proctor, 1993).

In this study, the IRP approach was adapted to investigate whether there is a fundamental difference in the processing of small numerosities (in the subitizing range) and larger numerosities, and whether any subitizing effect is distinct from the effects of pattern recognition. Participants were asked to perform a quantification task (is the presented quantity greater or less than?). This meant that different numbers could be assigned to the same response category (smaller than vs. larger than the comparator), but, within the same number category, contrasting repetition effects could be assessed. With both the smaller and larger numerosities, consecutive trials could have: (i) repeats of an identical pattern (the identitical repetition condition; note that, in some cases the pattern was shifted across space, to eliminate exact location repetition), (ii) repeats of the same number, but in a different pattern (number repetition trials), and (iii) repeats of a different quantity but from the same response category (category repetition trials). Given that these conditions, for small and large quantities respectively, all involve the same response, then any contrast in the size of the repetition effects cannot be due to differences in response selection, but must reflect the processes involved in numerosity judgements. Five experiments are presented with the same pattern of performance: (i) for small numerosities, category repetition is less effective than number repetition which in turn can be less efficient than pattern repetition; (ii) for larger numerosities, there can be effects of pattern recognition, but there is no difference between conditions with same and different quantities (number and category repeats). In addition, performance with large number displays varies according to whether consecutive displays have the same proportion of items with the same contrast polarity; in contrast, the effects of number repetition are unaffected by the similarity of the contrast polarity across consecutive smaller display sizes These data suggest that distinct numerical identities for the different small numbers displays are computed across trials, while the same approximate representation is computed for larger numbers. This approximate representation is sensitive to low-level visual similarities across displays.

Experiment 5.1: Basic effects.

Experiment 5.1 reports the basic pattern of priming effects that will be followed in the subsequent experiments. Participants were asked to determine the magnitude category that a given pattern belonged to and there were three categories: Small (1), Medium (3-5) and Large (7-9). The small category was introduced as a baseline condition. The medium and large categories each contained 3 numbers, allowing the following conditions to be created: (i) "*category repeat*" - in which consecutive displays contained different numbers of items, but the displays were assigned to the same response categories; (ii) "*identical repetition trials*" - where consecutive stimuli fell in exactly the same locations and had the same pattern; and (iii) "*same number repeats*" - consecutive displays contained the same number of items, but the items were repositioned. Larger repetition effects for identitical over same number repeat trials would indicate an effect of pattern similarity based on the orientation of the original patterns. Larger repetition effects for same number over same category repeats may reflect a benefit from repeating the process of assimilating the same exact number, though there may also be some contribution from pattern similarity if consecutive displays with the same number of items are more similar than consecutive displays with different numbers of items.

There were two sub-experiments. Experiment 5.1a reports the results with displays where the items are randomly presented in the field. In contrast to this, Experiment 5.1b tests effects with canonical dot patterns. Canonical patterns should maximise processes that might operate through form recognition and may be used with larger as well as smaller numerosity displays (cf. Mandler & Shebo, 1982). We expect effects of pattern similarity to be stronger in Experiment 5.1b than Experiment 5.1a.

Experiment 5.1a: Random patterns

Method

Stimuli

The stimuli used were displays of grey dots (RGB values: 190,190,190) on a black background. The dots had a diameter of 50 pixels and were presented on a 17 inch monitor with a 1024x768 pixel screen resolution. The experiment was made using E-prime v1.1 software (Schneider, Eschman, & Zuccolotto, 2002). The dots were drawn randomly within a 400x400 pixel window in the centre of the screen, with the restriction that items did not overlap and there was a minimum distance of 30 pixels between any two dots (see Figure 32).

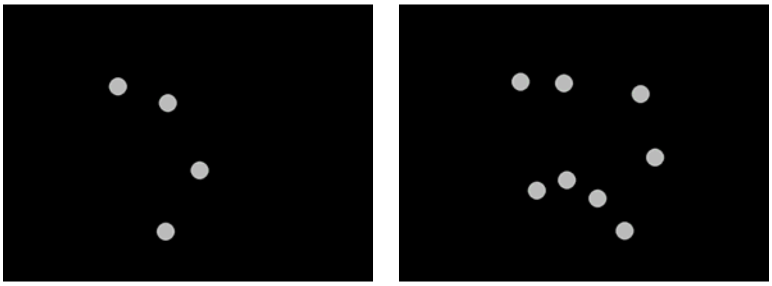


Figure 32. Example of a random dot displays in Experiment 5.1a.

Procedure

Each trial consisted of a fixation cross for 500 ms, followed by a dot display which stayed on until a response was made. The participants' task was to estimate the quantity class to which each display belonged as accurately and as fast as possible: Small – 1 dot-, Medium – 3 to 5 dots - and Large -7 to 9 dots-. Responses were made using the numeric pad (keys 1, 2 and 3).

The participants were seated so that they were approximately 50cm from the screen, but were allowed to move their head freely. Instructions were given on the screen, explaining the categories and requesting participants to make the correct response as quickly but as accurately as possible. A practice session consisting of 20 trials was conducted, so the participants felt comfortable with the stimuli and understood the task before data were recorded. During the experiment, participants had a break approximately every three minutes.

Design

The trial sequence was manipulated in order to introduce different kinds of repetition where, for the Medium and Large categories, consecutive items fell in the same response category. A *category repetition* was a repetition of the required category response, with a different numerosity (e.g. consecutive presentations of 7 and 8). A *number repetition* consisted of the same number of items across consecutive displays, but with different randomly-arranged patterns. On *identical repetition* trials, the exact same stimulus was repeated.

The repetition manipulation was introduced by pairing up the trials. The weights of the response repetition trials were adjusted so that there would be no response bias: participants were always more likely to receive two consecutive trials of different categories than of the same category. The occurrence of the three response categories was also evenly distributed across the trials. The repetition probabilities can be found in Table 4. Twelve participants from the University of Birmingham participated voluntarily for research credits. They completed the experiment in approximately 50 minutes and received a total of 2592 trials.

Table 4. Repetition probabilities in Experiment 5.1a.

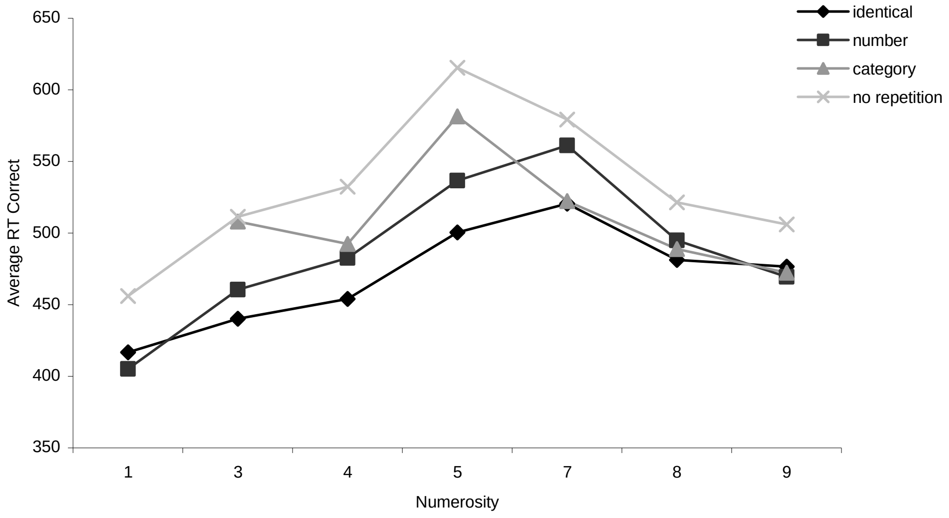
Condition	Random selection	Paired trial	Overall Probability
Identical repetition	0	2/9	0.1111
Number repetition	1/9	1/9	0.1111
Category repetition	2/9	1/9	0.2222
Different response	2/3	5/9	0.6111

Results

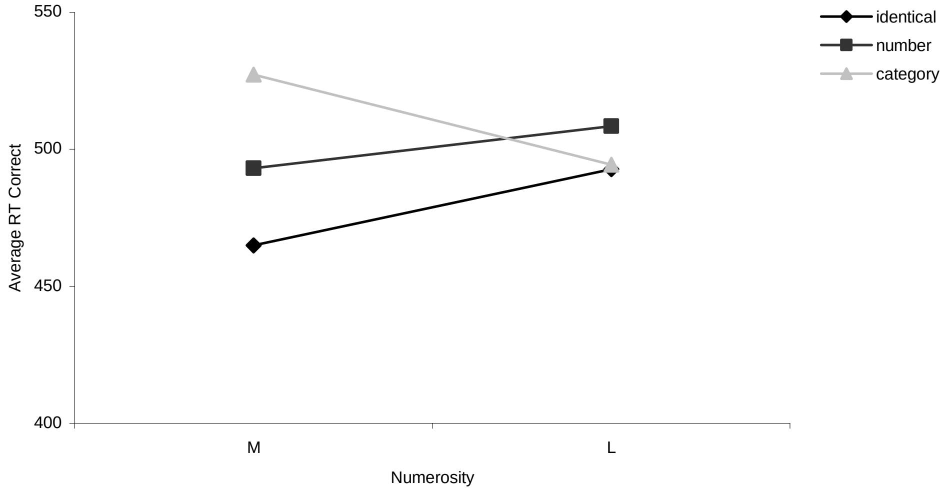
The analysis was restricted to trials that either had no repetition of the previous display (i.e. displays were from different response categories), or were a first repetition (from the immediately preceding trials only). All trials that occurred after more than 1 consecutive category response were rejected from the analysis (these occurred due to the random selection elements in the design). Due to this, the number of trials for each condition could vary across conditions and individuals. However, in every repetition condition for each participant, at least 15 trials per numerosity were left in the final datasets. In the experiment, both accuracy and reaction times were recorded. Analyses of reaction times (RTs) were restricted to correct responses. Trials where the RT differed by more than 3 standard deviations from the mean (in that condition for that participant) were left out of the analysis.

The mean proportions of errors for this and all the following experiments are provided in Table 7 (which can be found at the end of this chapter) In this experiment and in all the subsequent experiments the analysis of the errors demonstrated the same effects as the RT analysis. For this reason, and to save space, the analyses of the error data are not reported in full.

Responses to numerosity displays of 1 provide a baseline level of performance, but as they did not vary in the type of repetition involved (identical = number = category repetition), they were not entered in the main analysis. The effects of the categories, repetition types and numerosities were compared in a within subjects 2 x 3 x 3 ANOVA. The RT data are shown in Fig. 33. There was no overall difference between the two response categories ($F(1,11)= .203$, $p= .661$, partial $\eta^2= .018$). There were significant overall effects of the different types of response repetition ($F(2,22)= 6.875$, $p= .006$, partial $\eta^2= .385$), and the different numerosities ($F(2,22)= 9.313$, $p= .005$, partial $\eta^2= .458$). There were reliable interactions between response category and repetition type (F(2,22)= 9.299, p= .003, partial η²= .458) and between response category and numerosity (F(2,22)= 59.588, p<.001, partial η²= .844). There was no reliable interaction between repetition and numerosity (F(4,44)= .893, p= .476, partial η²= .075), and no significant 3 way interaction (F(4,44)= 1.818, p= .181, partial η²= .142).



(a)



(b)

Figure 33. RTs (ms) for correct responses in Experiment 5.1a. (a) mean RTs for each numerosity and repetition condition within each response category; (b) mean RTs for the different repetition conditions in each response category (averaged over the numerosities).

The repetition effects in the Medium and Large categories were assessed irrespective of numerosity. For the smaller numerosities (respond Medium), there was a reliable effect of the different repetition types (F(2,22)= 14.780, p<.001, partial η^2= .573). This was driven by differences between each repetition condition: identical repetitions were responded to faster than number repetitions (F(1,11)=5.348, p= .041, partial η^2=.327) and category repetitions (F(1,11)= 28.558, p< .001, partial η^2=.722). Number repetitions were responded to faster than category repetitions (not the same numerosity) (F(1,11)= 10.540, p= .008, partial η^2= .489). In the Large category, there were no differences between RTs for the different repetition conditions (F(2,22)= 1.104, p= .347, partial η^2= .091).

The interaction between response category and numerosity was investigated by assessing the effects of different numerosities within each category, irrespective of repetition type. In the Medium (3-5) category the effect of numerosity (F(2,22)= 56.624, p< .001, partial η^2= .837) was due to slower RTs to display size 5 compared with display sizes 3 (F(1,11)= 78.583, p< .001, partial η^2= .877) and 4 (F(1,11)= 83.720, p< .001, partial η^2= .884). Display sizes 3 and 4 did not differ. In the Large (7-9) category, the effect of numerosity (F(2,22)= 22.762, p< .001, partial η^2= .674) reflected the speeding of RTs as the display sizes increased: 7>8 (F(1,11)= 29.586, p< .001, partial η^2= .729), 7>:9 (F(1,11)= 25.207, p< .001, partial η^2= .697) and 8>9 (F(1,11)= 4.945, p= .048, partial η^2= .310).

Discussion

There were several important results. First, there was clear evidence for carry-over effects across trials. Second, the carry-over effects differed for the small (respond Medium) and large (respond Large) display sizes. For the small display sizes, there was an advantage for identical pattern repetitions over a new random arrangement of the same number of items (the number repetition condition) and over performance when consecutive displays had different numbers belonging to the same response categories. There was also a benefit for same number trials over same category trials. For large display sizes, performance did not vary across the repetition conditions.

For the small display sizes, the same identity advantage can be attributed either to a repeat of the same pattern or to a repeat of the same locations being filled across trials. The advantage for same number over same category trials may also be due to the same number displays having greater visual similarity than the same category displays (Logan & Zbrodoff, 2003). Alternatively, this last result may be due to the same exact value being computed in the same number condition, whereas different number values are computed across trials in the category repeat condition. Sensitivity to exact number may reflect the operation of a subitization process based on parallel assimilation of the elements (Trick & Pylyshyn, 1989), rather than pattern recognition. The subitization and pattern similarity accounts are examined further below. For both accounts, performance may be expected not to differ across the repetition conditions for the larger display sizes. For the pattern recognition account, different patterns may not be discriminable at the larger display sizes, so that effects of pattern repetition are equal in the same identity, same number and same category conditions. For the subitization account, exact number cannot be computed for the larger display sizes without counting, so performance may depend on an estimated representation where only approximate number is coded. This approximate representation does not differentiate between the three repetition conditions.

Experiment 5.1b was designed to enable pattern recognition to play a stronger role than in Experiment 5.1a. In Experiment 5.1b, the displays contained familiar patterns for all numerosities, enabling pattern recognition processes to come into play for both small and large display sizes alike (Wolters et al., 1987; Lassaline & Logan, 1993; Palmeri, 1997). Stronger effects of pattern recognition should be confirmed by a larger advantage emerging for the same identity condition over the other repetition conditions. If pattern recognition is crucial to the advantage for same number over same category trials, then this difference should be apparent for the larger numerosities in Experiment 5.1b as well.

Experiment 5.1b: Canonical displays

Method

Familiar patterns of dots were created using Photoshop, so that the inter-dot distance was always 50 pixels (the same as the dot diameters). The images were saved in bitmap format and loaded into the E-prime experiment (see Figure 34 for an example of the displays used).

Figure 34. Examples of displays used in Experiment 5.1b

In this experiment, a *category repetition* trial again involved repetition of the required category response, with a different numerosity (e.g. consecutive presentations of 7 and 8). A *number repetition* consisted of a 45 degrees rotation of the pattern in the previous trial. Finally, on *identical repetition* trials, the exact same stimulus was repeated.

The probabilities for the different repetition conditions are given in Table 5. Twelve participants from the University of Birmingham participated voluntarily for research credits. They completed the experiment in approximately 50 minutes and received a total of 2304 trials.

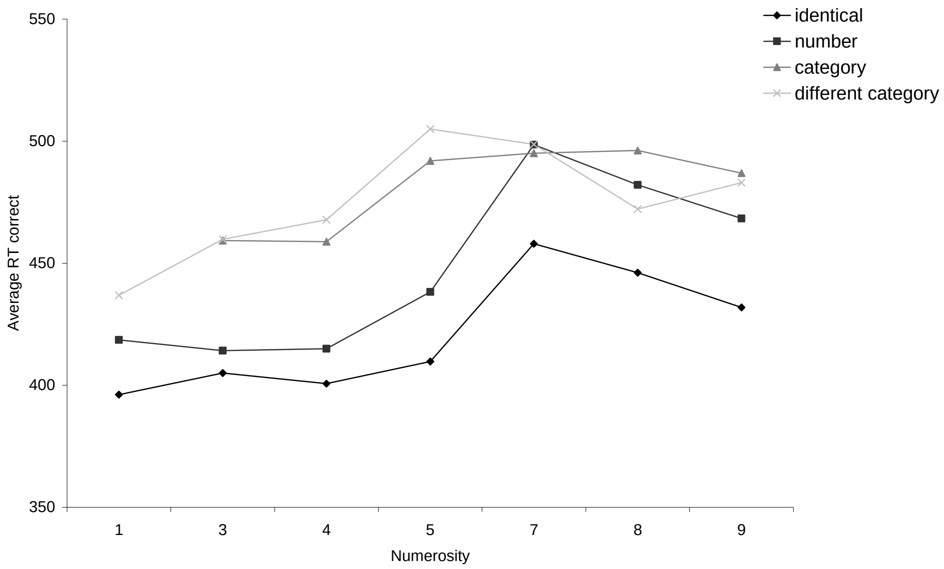
Table 5. Repetition probabilities in Experiment 5.1b.

Condition	Random selection	Paired trial	Overall Probability
Identical repetition	1/18	1/8	0.0903
Number repetition	1/18	1/8	0.0903
Category repetition	4/18	1/8	0.1736
Different response	2/3	5/8	0.6459

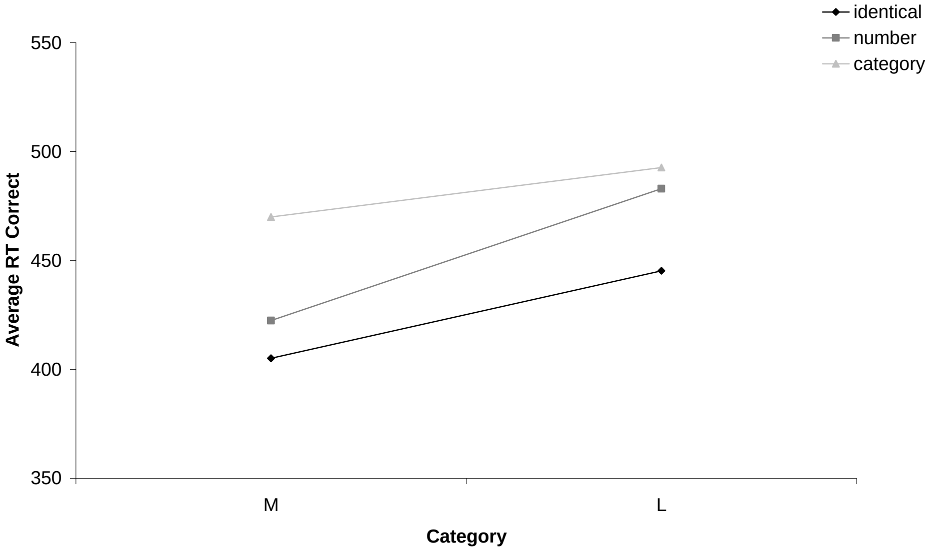
Results

The data were prepared as for Experiment 5.1a. The mean proportions of errors are again provided in Table 7 .

The effects of the categories (M and L), the repetition types (category, number or exact) and the numerosities (s, m, l, within the M and L response categories) were compared in a within subjects 2 x 3 x 3 repeated measures ANOVA of the RT data, using same response trials only (see Figure 35). There was a significant main effect of category (F(1,11)=13.263, p= .004, partial η^2= .547), with faster responses to the Medium category, and of repetition type (F(2,22)= 31.699, < .001, partial η^2= .742), but no significant main effect of numerosity within each response category (F(2,22)= 1.182, p= .321, partial η^2= .097). There was a reliable interaction between category (M vs L) and repetition type (F(2,22)= 8.755, p=.004, partial η^2= .443), with the different repetition conditions having different effects for the smaller numerosities compared to the larger numerosities. There was also a signifigant interaction between category (M vs. L) and numerosity (s, m, l) (F(2,22)= 18.722, p<.001, partial η^2= .630), but not between repetition type and numerosity (F(4,44)= 1.132, p= .354, partial η^2= .093). There was also no significant 3 way interaction (F(4,44)= .245, p= .758, partial η^2= .022).



(a)



(b)

Figure 35. Reaction times (RTs) in Experiment 5.1b.(a) The full set of RTs for each repetition type for each numerosity within each category (small, medium and large, corresponding to 3,4 and 5 for the Medium category and 7,8 and 9 for the Large category). (b) Mean RTs for the repetition types in both categories (averaged over the different numerosities).

The interaction between category and repetition type was decomposed by assessing the different types of repetition within each category separately, irrespective of the numerosities. In the Medium category there were significant main effects of repetition

($F(2,22)=44.873$, $p<.001$, partial $\eta^2= .803$). Reaction times (RTs) on the smaller numerosities were faster for identical compared to number repetitions ($F(1,11)=18.332$, $p= .001$, partial $\eta^2= .625$), as well as compared to category repetitions ($F(1,11)= 54.173$, $p< .001$, partial $\eta^2= .831$); RTs were also faster for number than for category repetitions ($F(1,11)=39.810$, $p<.001$, partial $\eta^2= .784$).

In the Large category, there was also a significant main effect of the different repetition conditions ($F(2,22)= 13.925$, $p<.001$, partial $\eta^2= .559$). RTs were faster for identical relative to number repetitions ($F(1,11)=16.077$, $p= .002$, partial $\eta^2= .594$) and relative to category repetitions ($F(1,11)= 13.830$, $p= .003$, partial $\eta^2= .557$). RTs on number repetitions were marginally faster than category repetitions ($F(1,11)=4.891$, $p= .049$, partial $\eta^2= .308$).

When only number and category repetitions are considered for the Medium and the Large response categories, there remained a highly significant interaction between repetition and category ($F(1,11)= 36.516$, $p< .001$, partial $\eta^2= .768$). The advantage for number over category repetitions was greater for the smaller numerosities than the larger numerosities.

When only identical and number repetitions are considered for the Medium and the Large response categories, there was a marginal interaction between the two types of repetition and the response category ($F(1,11)= 3.923$, $p= .073$, partial $\eta^2= .263$). There was a trend for the advantage for identical over number repetitions to be greater for the larger than the smaller numerosities.

The interaction between category (M, L) and numerosity (s, m, l) was investigated by assessing the effects of the different numerosities within each category separately, irrespective of repetition type. For the Medium category, there was a significant effect of numerosity ($F(2,22)= 14.578$, $p= .002$, partial $\eta^2 =.570$). There was no difference in RT between numerosities 3 and 4 ($F(1,11)= .689$, $p= .424$, partial $\eta^2= .059$), but slower RTs for numerosity

5 compared to 3 (F(1,11)= 15.563, p= .002, partial η^2= .586) and to 4 (F(1,11)= 14.917, p= .003, partial η^2= .576). This is likely to reflect an increased difficulty as the numerosities get closer to the dividing criterion (below or above 6). Data for the Large category presented a mirror picture. The significant effect of numerosity (F(2,22)= 6.845, p= .006, partial η^2= .384) here was due to RTs being slower for numerosity 7 (close to the dividing criterion) compared to 9 (far from the criterion)(F(1,11)= 12.802, p= .004, partial η^2= .538). The intermediate contrasts were not reliable (7 vs. 8, 8 vs. 9).

Discussion

The basic pattern of results was similar to that observed in Experiment 5.1a. There were effects of repetition, and these effects differed for small (respond Medium) and large display sizes. For both display sizes, there was an advantage for same identity over the other repetition conditions, but this effect tended to be stronger for the larger display sizes. There was also an advantage for same number over category repetition trials, but, in contrast to the effects of repeating the same identity, the same number advantage was greater for small relative to large display sizes.

The emergence of a same identity advantage for larger display sizes in Experiment 5.1b is consistent with participants being able to enumerate larger displays on the basis of familiar canonical patterns (see Manddler & Shebo, 1982) and it provides evidence that pattern recognition can contribute to performance. When the same pattern is repeated across consecutive trials, participants can respond using the same representation, speeding their responses. However, despite participants using the same identity displays to facilitate responses, there was only a modest advantage for same number over same category displays in the larger displays. This would occur if the contrasting patterns were not sufficiently different at the larger display sizes to differentiate between same number and same category trials. Across the smaller display sizes there was only a modest same identity advantage and a relatively strong same number advantage (compared with the category repeat condition). This different pattern of results may be because, at small display sizes, the similarity between identical displays does not differ greatly from that between non-identical displays with the same numbers of stimuli (in the same number condition), and, in both cases, displays are more similar than when consecutive displays have different numbers of items (in the category repeat condition). Alternatively, the contrast between small and large display sizes may arise because only small displays can be subitized on the basis of parallel processing of their elements. RT differences emerge for small display sizes in the same number and same category displays because number values are constant in the first instance but differ in the second. These views are considered in further detail in Experiment 5.3, where participants rated the similarity of the displays in the different conditions. Prior to this, however, Experiment 5.2 was performed in order to rule out other potential factors that could have contributed to the different results for small and larger numerosity displays.

Experiment 5.2: Controlling for display area and response criteria

In Experiment 5.1b the surface occupied by the dot pattern increased in size as the numerosities increased. It is possible that participants based their judgments on the size of the occupied area rather than on number magnitudes and this might have affected performance particularly at the larger numerosities, reducing effects of exact number on performance (e.g., if particuipants simply responded ‘large’ when the items covered a large area). To eliminate this possibility Experiment 5.2a assessed the effects of stimulus repetition on displays that always occupied the same surface area. (Note that the random dot patterns in Experiment 5.1a did not necessarily increase in surface are with increasing numbers, however, as the patterns were random, this was not strictly controlled for.)

Experiment 5.2b attempted to rule out another possible confounding factor due to the Method in Experiment 5.1. In Experiment 5.1, the response categories were set up so that the small number category (Medium) was in the middle of the range of categories that were used. Conceivably this might have made participants more conservative to respond to members of this response category, since it was bordered at two extremes by other response categories (Small and Large). If a check process was generated for this Medium category when consecutive displays had different numbers of items (in the repeat category condition), the repeat category condition would be relatively slow for the smaller display sizes (respond Medium) compared with the larger displays (respond Large). To ensure that the previous results were not due to this, the numerosity judgement was changed in Experiment 5.2b, so that the response category for small numerosities was at an extreme end. If the differential repetition effects for number over category repeats, for small but not larger display sizes, is not due to confounds based on the display area or to the range of responses used, then performance in both Experiments 5.2a and b should resemble the pattern of results in Experiment 5.1.

Experiment 5.2a: Display area

Method

In order to have the same surface occupied by all the numerosity displays, but still have standard dot patterns, rather than random organisations, we used circular dot displays. These displays were drawn within E-prime so that the dots would be equally distributed on an invisible 200 pixel radius circle. The resulting patterns were random rotations of standard patterns with equal spacing between the dots on the circle.

The definitions of the repetition conditions (identical, number, category and no repetition) were the same as in Experiment 5.1, except that the *number repetition* here was a random rotation of the circular pattern from the previous trial –See Figure 36 for an example. The weighting of the paired repetition conditions was the same as in Experiment 5.1a. The probabilities can be found in Table 4. Twelve participants from the University of Birmingham participated voluntarily for research credits. They completed the experiment in approximately 50 minutes and received a total of 2592 trials.

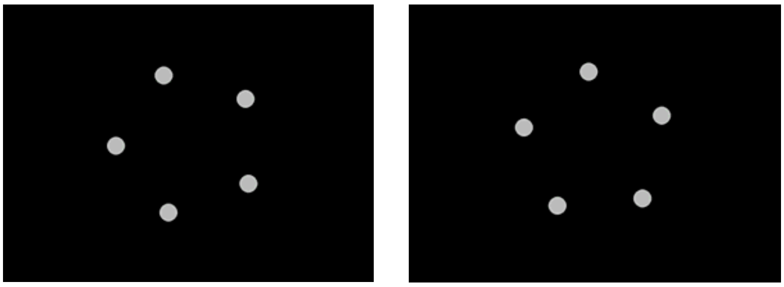


Figure 36. Example of a number repetition used in Experiment 5.2a

Results

The error data followed the same pattern as RTs and there were no signs of a speed-error trade-off. The data are presented in Table 7. The RT data for correct responses were pre-processed in the same way as in Experiment 5.1. These preprocessed RT results are presented in Figure 37. The effects of the categories, the repetition types, and the numerosities were compared in a within subjects 2 x 3 x 3 ANOVA. There was no overall difference in RT between the two response categories (F(1,11)= .186, p= .675, partial η^2= .017). There were significant main effects of the different types of repetition (F(2,22)= 16.926, p< .001, partial η^2= .606), and of the different numerosities within the response categories (F(2,22)= 8.655, p=

.002, partial η²= .440). There were reliable interactions between the response category and the type of repetition (F(2,22)= 33.679, p< .001, partial η²= .754), between the response category and the actual numerosities (F(2,22)= 16.347, p< .001, partial η²= .554) and between the repetition type and the numerosities (F(4,44)= 5.493, p= .012, partial η²= .333). There was no reliable 3 way interaction (F(4,44)= 1.647, p= .205, partial η²= .130).

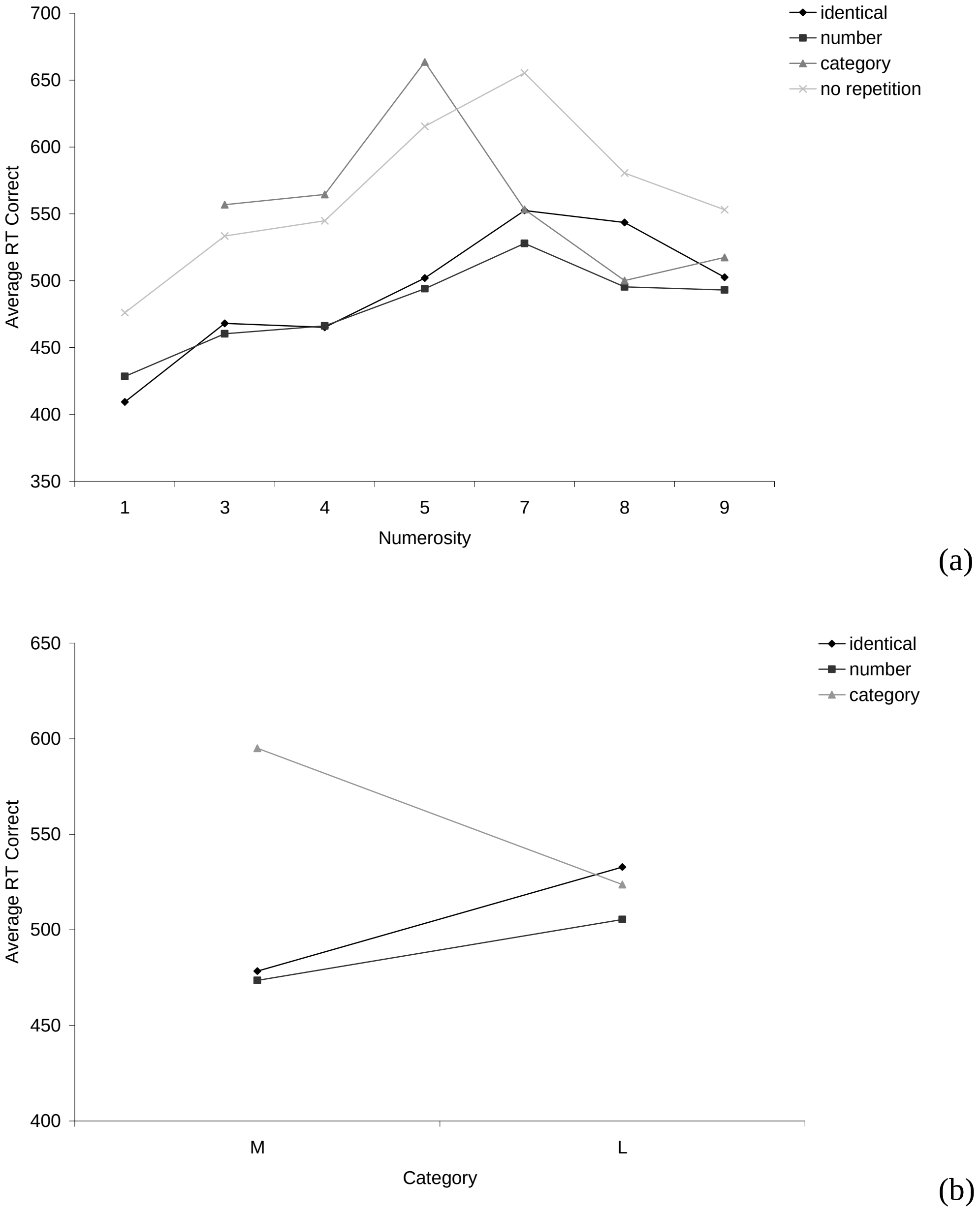


Figure 37. Reaction times in Experiment 5.2a.(a) The full data shown for each response category, numerosity and repetition condition. (b) The average RTs per repetition condition for the medium and large categories.

The effects of the different types of response repetition were assessed for the Medium and Large categories separately, irrespective of the numerosity. In the Medium category there was a significant main effect of repetition type ($F(2,22)= 34.587$, $p< .001$, partial $\eta^2= .759$). RTs were significantly faster on identical repetitions compared to category repetitions ($F(1,11)= 35.781$, $p< .001$, partial $\eta^2= .765$) and faster on number repetitions compared to category repetitions ($F(1,11)=36.443$, $p<.001$, partial $\eta^2= .768$). There was however no significant difference between identical and number repetitions ($F(1,11)= .653$, $p= .436$, partial $\eta^2= .056$). In the Large category, there were no differences in RTs as a function of the different types of response repetition ($F(2,22)= 2.215$, $p= .133$, partial $\eta^2= .168$).

The interaction between response category and numerosity was broken down to assess the effects of the numerosity in each of the response categories, irrespective of the repetition types. For the Medium category, there was a significant effect of numerosity ($F(2,22)= 14.638$, $p< .001$, partial $\eta^2 = .571$). There was no difference in RT between numerosities 3 and 4 ($F(1,11)= .133$, $p= .722$, partial $\eta^2= .012$), but reliable differences between 3 and 5 ($F(1,11)= 25.996$, $p< .001$, partial $\eta^2= .703$) and 4 and 5 ($F(1,11)= 13.991$, $p= .003$, partial $\eta^2= .560$). For the Large category, there was also a significant effect of numerosity ($F(2,22)= 9.065$, $p= .002$, partial $\eta^2= .452$), with slower RTs for 7 than 9 ($F(1,11)= 15.116$, $p= .003$, partial $\eta^2= .579$), and 8 ($F(1,11)= 12.464$, $p= .005$, partial $\eta^2= .531$); RTs for 8 and 9 did not differ ($F(1,11)= .686$, $p= .425$, partial $\eta^2= .059$).

Finally, the interaction between the repetition types and the numerosities occurred because the difference between the repetition conditions tended to be larger for display size 5, however, as indicated above, category repetitions were slower than the other repetition conditions for all display sizes within the medium category.

Discussion

The same general pattern of results was found as in Experiment 5.1. In particular, the difference between number and category repetitions for the small display sizes (Medium response category) remained highly significant, while here there was no difference across these conditions for the Large response category. For neither display size were there reliable benefits for the same identity condition over the other repetition conditions. The failure to find a same identity advantage here occurred even though canonical patterns were presented at all display sizes (due to the inter-element spacing being kept constant). Howevere, it may be that, with the circular displays, differences between the patterns decreased. This may be sufficient to lose the differential repetition effects at the larger display size. It may also be sufficient to equate performance with same identity and same number displays at rhe smaller display size. Whatever the case, the important result is that the differential pattern of performance with small and large displays was maintained, though the display area was equated.

Experiment 5.2b: Controlling for a possible effect of the middle category.

In Experiment 5.1 and 5.2a, the crucial “Medium” category was in the middle of the range of categories that were used. To ensure that the previous results were not due to a different approach to the middle response category, the numerosity judgement was changed for Experiment 5.2b so that the smaller numerosities comprised the Small response category, the Medium response category was made up of larger numerosities and the Large response category comprised even larger display sizes. If the differential repetition effects for number over category repeats for small displays (Medium category) in Experiments 5.1 and 5.2a were due to this category falling in the middle of the range, then we should find similar effects here for display sizes 6-8, which again comprise the Medium category. On the other hand, if the differential repetition effects only occur with small, subitizable numbers, then the differential repetition effects should be found only with the Small category.

Method

The response categories were re-designed so that numerosities of 2, 3 and 4 now formed the ‘Small’ category, ‘Medium’ was 6 to 8 and ‘Large’ 15 to 17. These values were chosen to reflect the same perceivable difference between the increasing categories according to Weber’s law (based on the middle of each category). The response keys corresponded to keys for 1, 2 and 3 on the numeric pad. The numerosity displays remained the same circular pattern displays occupying a constant surface area (see Method Experiment 5.2a) for all numerosities. The resulting patterns were random rotations of circular patterns with equal spacing between the dots on the imaginary circle (for an example of displays belonging to the 3 different response categoryies, see Figure 38). The definitions of the repetition conditions (identical, number, category and no repetition) were the same as in Experiment 5.2a..The weighting of the paired repetition conditions was also the same as in Experiment 5.2a. Twelve students from the University of Birmingham participated voluntarily for research credits. Each participant received a total of 2592 trials.

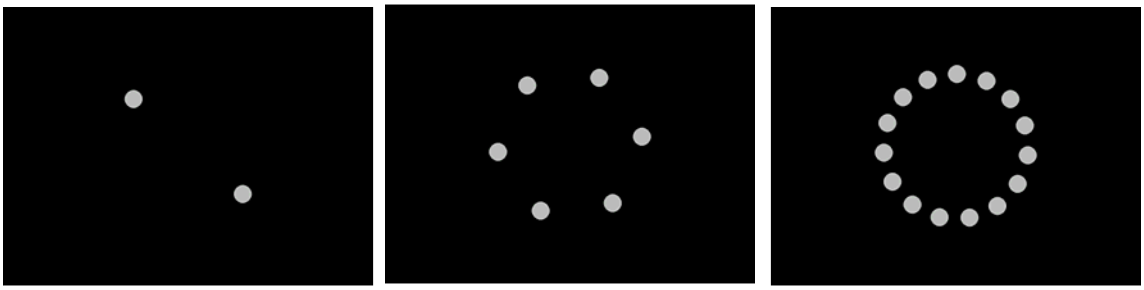


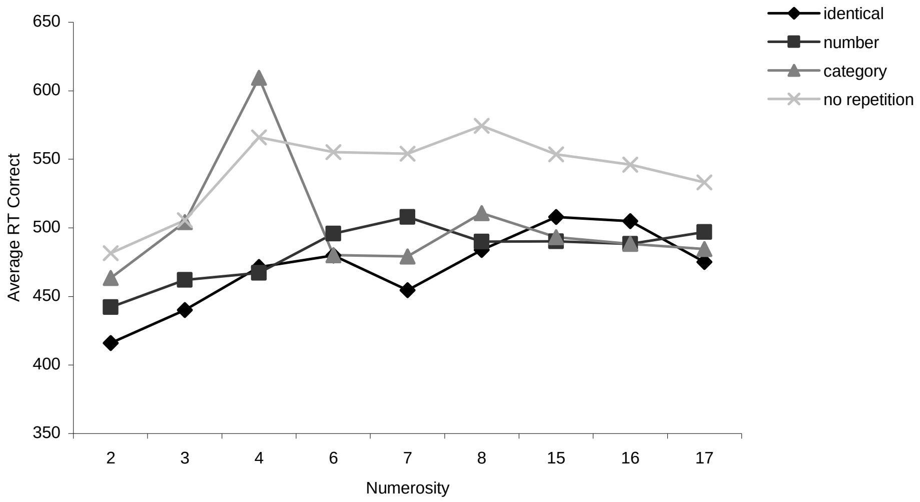
Figure 38. Examples of displays in the small, medium and large response categories in Experiment 5.2b.

Results

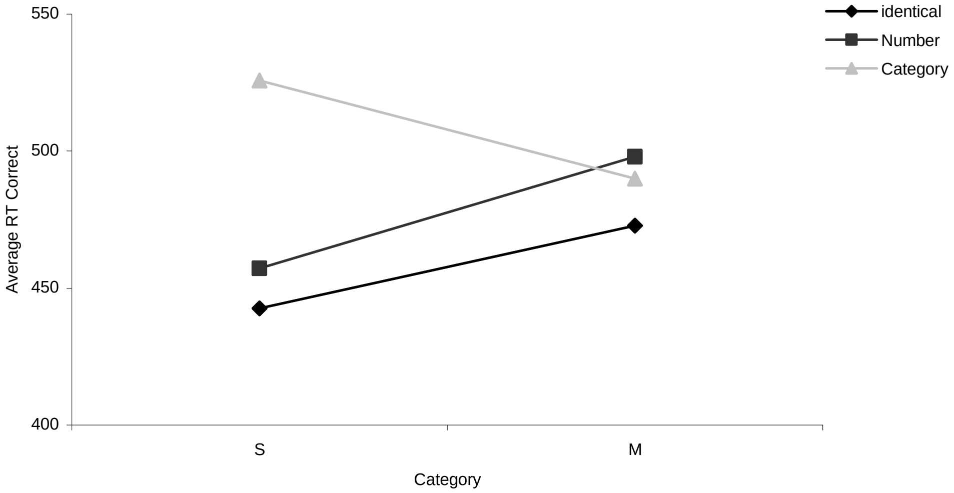
The data were pre-processed in the same way as in the previous experiments. The accuracy results are presented in Table 7. The errors followed the same trends as the RT data and there were no signs of any speed-accuracy trade-offs.

To allow for comparison with the previous experiments, only the Small and Medium categories were included in the RT analyses. This resulted in a within subjects 2 x 3 x 3 ANOVA (response categories, repetition types and numerosities within each response category). There were significant main effects of the types of response repetition ($F(2,22)= 46.218$, $p< .001$, partial $\eta^2= .808$), as well as overall effects of the specific numerosities ($F(2,22)= 35.504$, $p< .001$, partial $\eta^2= .763$), but no reliable overall difference in RTs on the (new) Small and Medium response categories ($F(1,11)= 2.064$, $p= .179$, partial $\eta^2= .158$).

There were reliable interactions between response category and repetition type ($F(2,22)= 33.195$, $p< .001$, partial $\eta^2= .751$), response category and numerosity ($F(2,22)= 17.877$, $p<.001$, partial $\eta^2= .619$) as well as the different repetition types and numerosity ($F(4,44)= 11.936$, $p< .001$, partial $\eta^2= .520$). There was also a significant 3 way interaction ($F(4,44)= 3.525$, $p= .037$, partial $\eta^2= .243$). The data are shown in Figure 39.



(a)



(b)

Figure 39. RT (ms) on correct responses in Experiment 5.2b. (a) The average RTs for each response category, repetition condition and numerosity. (b) The different repetition effects in the critical Small (2-4) and Medium (6-8) response categories..

The interactions were further investigated by assessing the effects of the different types of repetition and numerosity within each category. In the Small (2-4) category there were significant main effects of repetition type ($F(2,22)= 74.940$, $p< .001$, partial $\eta^2= .872$) and numerosity ($F(2,22)= 51.729$, $p<.001$, partial $\eta^2= .825$) and a reliable interaction between numerosity and repetition type ($F(4,44)= 13.389$, $p= .001$, partial $\eta^2= .549$). RTs were significantly faster for identical repetitions, compared to number repetitions ($F(1,11)= 19.635$, p= .001, partial η^2= .641) and compared to category repetitions (F(1,11)= 103.399, p< .001, partial η^2= .904). RTs were also faster for number repetitions than for category repetitions (F(1,11)= 58.703, p<.001, partial η^2= .842). The slower RTs in the category repetition trials were particularly pronounced for display size 4 (Figure 39), and this was the source of the 3-way interaction. Nevertheless the contrast between the number and category repetition conditions was significant for display sizes 2 and 3 also. Taking just these display sizes, there were still significant effects of repetition type (F(2,22)= 28.121, p< .001, partial η^2= .719) and there were reliable differences between identical and number repetitions (F(1,11)= 47.533, p< .001, partial η^2= .812), identical and category repetitions (F(1,11)= 47.320, p< .001, partial η^2= .811), and between number repetitions and category repetitions (F(1,11)= 11.263, p= .006, partial η^2= .506).

In the Medium (6-8) category, there was a significant main effect of repetition type (F(2,22)= 6.074, p= .008, partial η^2= .356), but no significant effect of number (F(2,22)= 1.817, p= .191, partial η^2= .142), and no reliable interaction (F(4,44)= 2.661, p= .070, partial η^2= .195). RTs were faster with identical repetitions than with both number repetitions (F(1,11)=11.109, p= .007, partial η^2= .502) and category repetitions (F(1,11)= 5.407, p= .040, partial η^2= .330), but there was no significant difference between number and category repetitions (F(1,11)=1.234, p= .290, partial η^2= .101).

Discussion

The pattern of results matched that in Experiments 5.1 and 5.2a, even though the response categories here were changed so that the ‘Medium’ category (display sizes 6-8) covered numerosities previously in the large category. In the present case there were differential effects of number vs. category repetition for the small (2-4) category but not for the medium category (6-8). On a subitization account, responses to consecutive small display sizes are sensitive to repetitions of the same exact number, whereas responses to consecutive large display sizes (above the subitization range) are sensitive to repeats of the same approximate magnitude (the same for number and category repeats). Alternatively the differential effects could stem from differences in pattern similarity in the same number and category repeat conditions with small and large display sizes (Logan & Zbrodoff, 2003).

Interestingly, performance was poor on numerosity 4 in the present study. In contrast, in Experiments 5.1 and 5.2, there was a drop in performance on numerosity 5. These data suggest that the decisions were slowed when a given numerosity was close to the decision criterion. It should also be noted that there was no trend here for RTs to decrease as the display sizes increased from 6 to 8, although this was observed in Experiments 5.1 and 5.2. Again, this points to RTs reflecting the distance to the decision boundary, since, in the current experiment, the medium displays were flanked by ‘small’ and ‘large’ decision boundaries, flattening RTs across this category. Nevertheless, the critical point is that the differences between the small and larger display sizes remained here, even though participants now categorised the larger display sizes as falling in the middle of the range of displays.

Experiment 5.3: Effects of visual similarity

In discussing the data from Experiments 5.1 and 5.2, two different proposals have been made for the different effects of stimulus repetition at the smaller and larger display sizes. On one account, carry-over effects are influenced by visual similarity between consecutive displays. RTs are speeded if consecutive displays are similar and slowed if they are dissimilar. According to this account, small display sizes are similar in the same identity and same number conditions, and dissimilar in the category repeat condition; larger display sizes are equally similar across the different repetition conditions. Alternatively a subitization account holds that exact number can be computed from parallel processing of a small number of elements. For small display sizes, number values stay constant in the same number condition and this facilitates performance relative to when exact number values differ (in the category repeat condition). For larger display sizes, approximate rather than exact number representations are computed and, since these are the same across the repetition conditions, no differential repetition effects occur. These two accounts are not mutually exclusive, however, and both pattern similarity and subitization of exact small numbers may take place. Indeed Experiment 5.1b provided evidence for a contribution of pattern similarity when canonical patterns were used for large display sizes, so a ‘subitization only’ account does not seem viable. Nevertheless, for a pattern recognition account certain patterns of similarity are required for the data to be explained. For example, for small display sizes there need to be higher levels of similarity between displays having the same number of items than between displays with different numbers of items. In contrast, for large display sizes similarity levels should be roughly equivalent across the different repetition conditions and, for same category displays, similarity ratings should be higher for larger than for small display sizes. This was assessed in Experiment 5.3a, where we had participants rate the similarity of consecutive displays. The ratings were conducted on displays where we measured numerosity judgements in Experiments 5.3b and c. Unlike the earlier experiments, the items in these experiments could have different contrast polarities relative to their background. This allowed us to introduce a new factor – whether consecutive displays had the same or different proportions of items with the same contrast polarity. Visual similarity should be higher when consecutive displays maintain their relative contrast polarities (e.g., there are the same numbers of dark to light grey items), relative to when the relative contrast polarities differ - a result which the rating study confirmed for the same number condition. Given this, then effects of visual similarity should be stronger when the contrast polarities of consecutive displays stay the same compared with when they differed. This was tested in Experiments 5.3b and c.

Experiment 5.3a: Similarity ratings for the different repetition types

Method

Experiment 5.3a used paired presentations of the different response repetition trials, as well as paired presentations of different category trials, and participants were asked to rate the pattern similarity of the two images. Ratings were on a linear scale from 1 (very dissimilar) to 9 (exactly the same). The dot displays were made up of random proportions of darker and lighter dots presented against a grey background. The background was grey (RGB: 127,127,127) and a random proportion of each set of items that were to be displayed (ranging from 0 to the full quantity) were coloured lighter grey (RGB:204,204,204) and the rest were darker grey (RGB: 50,50,50). For an example of the stimuli, see Figure 40.

Figure 40. Examples of displays in Experiment 5.3.

There were four types of repetition for each numerosity (3,4,5 and 7,8,9): (i) same identity (consecutive stimuli were exactly the same in both number, position and contrast polarity); (ii) same number, same polarities (consecutive displays had the same number of elements and the number of dark and light grey items were maintained, but the locations of the items was randomised across trials); (iii) same number, different polarities (consecutive displays had the same number of elements but they had different proportions of dark and light grey items and the locations of the items was randomised across trials), and (iv) same category - the items present differed in number, proportion of dark and light grey elements and location, but remained in the same response category as for the numeerosity judgement experiments. In addition, in a fifth pairing consecutive displays had different numbers of dots drawn from different response categories (displays differed also in the proportions of dark and light grey elements and in the positions of the elements).

After the participants were given the instructions, the rating procedure was the following: a fixation cross appeared for 1000ms, followed by the first dot pattern for 500ms, then another fixation cross for 200ms and then the second dot pattern appeared and stayed on the screen for 500ms again, this was followed by a blank screen for 300ms and then the response screen came up asking the participant to rate the similarity of the two displays on a scale from 1 to 9.

Twenty five participants from the University of Birmingham took part voluntarily for research credits. They received a total of 786 trials divided over six blocks with breaks between each block.

Results

The average ratings per numerosity and repetition condition are given in Figure 41. The data were analyzed using a 4 (repetition conditions, not considering the different category pairs) x 2 (categories: Small vs Large) x 3 (numerosities in each category) within subjects repeated measures ANOVA. There was a reliable main effect of type of repetition ($F(3,72)= 558.022$, $p<.001$, partial $\eta^2= .959$) but no overall difference between the Small and Larger categories and no overall effect of the different numerosities. There were also significant interactions between: repetition condition and category (F(3,72)= 10.670, p< .001, partial η²= .308), repetition condition and numerosity (F(6,144)= 4.582, p= .002, partial η²= 0.160), and category and numerosity (F(2,48)= 50.722, p< .001, partial η²= .679). The 3-way interaction was also reliable (F(6,144)= 8.158, p< .001, partial η²= .254).

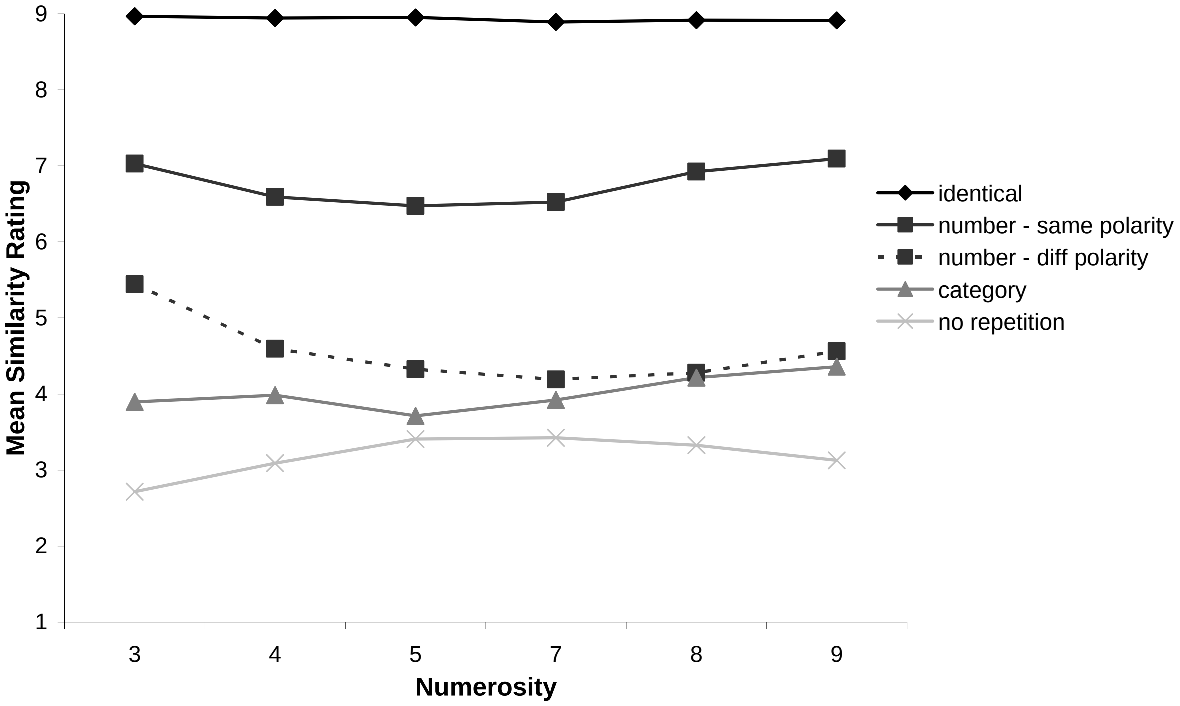


Figure 41. Average ratings per numerosity for the different repetition conditions using heterogeneous dot displays.

The 3-way interation was broken down by making different comparisons across the small and larger display sizes (3-5 and 7-9). A comparison of the same identity and same number, same polarity conditions showed higher ratings for the same identity condition (F(1,24)= 358.124, p<.001, partial η²= .937) but the ratings did not differ across the Smaller and Larger numerosities, as shown by the lack of a reliable interaction between the repetition conditions and the categories (F(1,24)= 2.240, p= .15, partial η²= .085).

A comparison across the two same number conditions did however reveal an interaction with category ($F(1,24)= 13.115$, $p= .001$, partial $\eta^2= .353$). There was no difference in the ratings for small and larger display sizes when the proportions of dark and light dots remained the same ($F<1.0$), but ratings were increased for small relative to larger displays in the same number condition when the displays had different proportions of dots ($F(1,24)= 11.779$, $p= .002$, partial $\eta^2= .329$) .

A similar analysis was performed comparing the ratings for the same number, different polarity condition and the ratings for the same category condition. Again there was a reliable interaction between the two types of repetition and the Smaller and Larger numerosity categories ($F(1,24)= 33.500$, $p< .001$, partial $\eta^2= .583$). There was no effect of display size on ratings for the category repeat condition ($F<1.0$) but ratings for the same number, different polarity condition were higher for the small compared with the larger numerosities (see above).

Discussion

The rating data confirm that same identity displays are judged as more similar than same number displays, which are perceived as more similar than same category displays (see also Logan & Zbrodoff, 2003). However, there were few differences in the pattern of ratings across the small and large display sizes with one exception – which was that stimuli with the same number and different contrast polarities were judged as more similar for the small numerosities than for the larger numerosities.

For the pattern recognition account to explain the carry-over effects reported in Experiments 5.1 and 5.2, then similarity should be judged higher for small than large displays in the same number condition, and it should be judged higher for large than small displays for the repeat category condition; we did not find this (at least for the same polarity condition). This was not simply due to floor or ceiling effects in the ratings given that the same number and category conditions were given ratings in the mid-similarity range (Figure 42). The rating data are thus problematic for the argument that only pattern similarity contributes to the carry-over effects in the numerosity judgement task. The data also give rise to one new prediction, which concerns the effects of varying the relative contrast polarities of the displays. The perceived similarity of same number displays with different contrast polarities was greater for small than for large display sizes. Hence, under conditions where the contrast polarity of the displays changes, we should expect similarity effects to be more pronounced on small than on larger display sizes. This was assessed in Experiments 5.3b and c.

Experiment 5.3b: Repeating numerosities while changing their luminance pattern

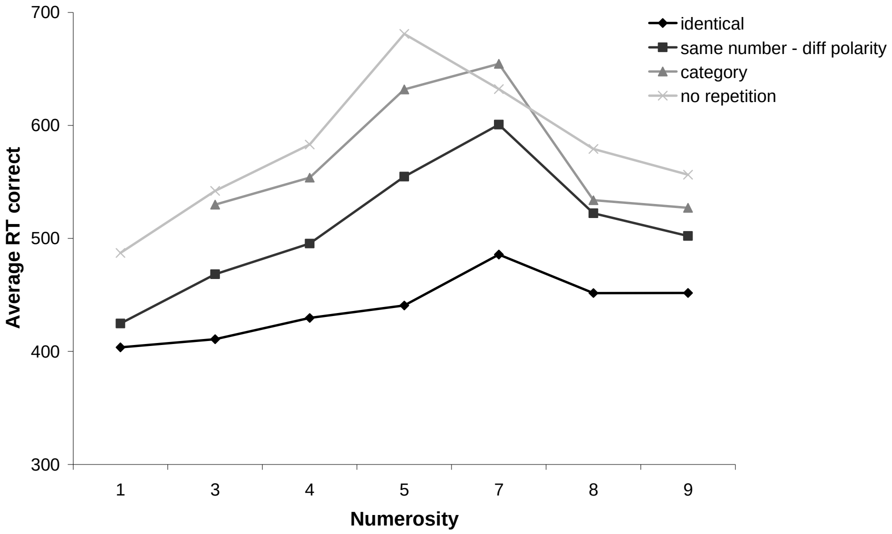
Method

The stimuli used were the same as those that were rated in Experiment 5.3a (see Figure 40 for an example). We again used the same serial reaction times repetition paradigm as before. On *identical repetition* trials, there was exactly the same pattern, with the same proportion of darker and lighter dots in the same location. On *number repetition* trials the same number of stimuli were presented but re-randomised into new locations and the proportion of light and dark grey dots was also re-randomised. On *category repeat* trials, the number of elements changed along with the dot locations and the proportion of darker and lighter dots.

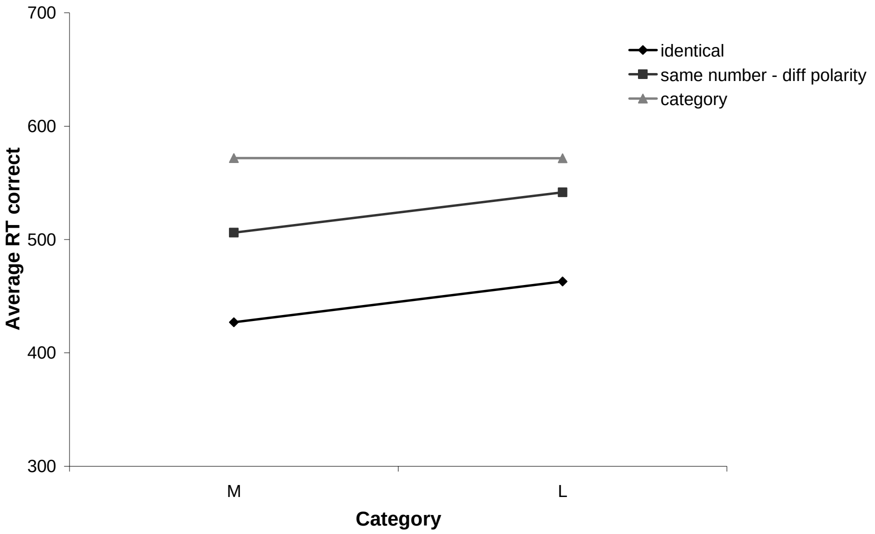
Sixteen participants from the University of Birmingham took part voluntarily for research credits. They completed the experiment in approximately 60 minutes and received a total of 2592 trials.

Results

The data were preprocessed in the same manner as before, with only first repetitions included and outliers in RTs left out of the analysis. The effects of the response categories, the repetition types (identical, number and category) and the numerosities were compared in a within subjects 2 x 3 x 3 ANOVA. The mean correct RTs are depicted in Figure 43. There were significant main effects of response repetition (F(2,30)= 52.268, p<.001, partial η²= .777), and overall effects of numerosity (F(2,30)= 5.526, p= .010, partial η²= .269) and response category (F(1,15)= 5.299, p= .036, partial η²= .261). There was a reliable interaction between response category and numerosity (F(2,30)= 26.482, p< .001, partial η²= .638). There was also a significant 3-way interaction (F(4,60)= 3.560, p= .039, partial η²= .192).



(a)



(b)

Figure 42. Reaction times on correct responses in Experiment 5.3b. (a) Data depicted as a function of all the numerosities for each response category and repetition type; (b) Data for the repetition effects within each response category, averaged over the constituting numerosities

.

To break down the 3-way interaction, the effects of repetition type and numerosity were assessed for the two response categories separately. For the smaller numerosities (in the 'Medium' response category) there were significant main effects of the type of repetition (F(2,30)= 49.504, p<.001, partial η^2= .767) and numerosity (F(2,30)= 18.443, p<.001, partial η^2=.551), and a reliable interaction between numerosity and repetition type (F(4,60)= 3.203, p= .037, partial η^2= .176). RTs were speeded for identical relative to number repeats (F(1,15)= 42.080, p<.001, partial η^2= .737) and category repeats (F(1,15)= 56.258, p< .001, partial η^2=.789) and for number relative to category repeats (F(1,15)= 37.289, p< .001, partial η^2=.713). RTs were also faster for display size 3 relative to display sizes 4 (F(1,15)= 6.365, p= .023, partial η^2= .298), and 5 (F(1,15)= 30.482, p< .001, partial η^2= .670), and for 4 relative to 5 (F(1,15)= 12.866, p= .003, partial η^2= .465). When the identical repetition condition was removed (but same number and category repeats included), the interaction between numerosity and repetition type disappeared (F(2,30)= .372, p= .687, partial η^2= .024) This interaction when identical patterns were included was due to the effects of the number of items being smaller in the same identity condition compared with the othere repetition conditions.

For the larger numerosities (‘Large’ response category), there were significant main effects of repetition type (F(2,30)= 23.611, p< .001, partial η^2= .612) and numerosity (F(2,30)= 18.871, p< .001, partial η^2= .557), but no interaction (F(4,60)= 1.759, p= .189, partial η^2= .105). There was no reliable difference between category and number repetitions (F(1,15)= 3.369, p=.086, partial η^2=.183), but identical repetitions were faster than both (F(1,15)= 31.590, p< .001, partial η^2= .678, and F(1,15)= 39.171, p< .001, partial η^2= .723, for category and number repetitions respectively). RTs decreased as the display size increased, with 7 >9 (F(1,15)= 18.854, p= .001, partial η^2= .557) and 7>8 (F(1,15)= 20.102, p< .001, partial η^2= .573).

If the results for the same identity and same number conditions are considered alone, then there was a main effect of repetition condition (F(1,15)= 56.066, p< .001, partial η^2= .789) and of category (F(1,15)= 10.758, p= .005, partial η^2= .418), but no interaction (F(1,15)= .002, p= .969, partial η^2= 0). The advantage for same identity over same number trials was equal for small and larger display sizes.

Discussion

These results again replicated the difference between number and category repetitions for small display sizes (in the Medium response category), whereas this difference was not present for the larger display sizes. The question is whether this differential repetition effect is due to greater visual similarity across small relative to large same number displays, or whether it is due to repetition of a common subitization process independent of visual similarity. The rating data indicated that participants judged that same number, different polarity displays were more similar when there were small display sizes compared to when there were larger display sizes. Thus this account correctly predicts that the same number condition here should be faster for small than for larger displays. However, when compared with the condition where the effects of visual similarity are maximized (with same identity displays), there was no advantage for same number displays with small relative to large display sizes. Based on the similarity ratings, the drop in the same number relative to the same identity condition should be reduced for small than for larger displays. It was not.

To provide another test of visual similarity effects, Experiment 5.3c was conducted. In this experiment the critical same number condition, consecutive displays always maintained the same proportions of dark to light grey items. The stimuli in this condition were rated as more similar than same number items when the proportions of dark to light grey stimuli changed (Experiment 5.1a). Hence RTs in this condition should be closer to those in the same identity condition. Critically, though, this should be matched across the smaller and larger display sizes, which were judged as having equally similar displays.

Experiment 5.3c: Heterogeneous dot displays with shifted same pattern trials

Method

This experiment used the same stimuli set up as Experiment 5.3a and b, with the numerosity displays being made up of random proportions of lighter and darker dots in random positions. The *same identity* repetition condition involved presentation of the same pattern, with the same proportion of darker and lighter dots in exactly the same locations. The *same number* condition this time had an identical proportion of darker and lighter dots as well as the same number of items across consecutive displays. The *category repeat* condition remained the same as in Experiment 5.3b. In addition to these conditions, a fourth same response condition was introduced. In this '*identity shift*' condition, the displays were equivalent to the same identity condition (consecutive displays had the same pattern and the same number of dark and light grey items) but the pattern as a whole was shifted across the field (so the dots no longer fell on identical retinal positions). The pattern was shifted by 100 pixels, either to the left, or right (1/2 probability). This new condition tests whether the benefits in the same identity condition reflect a repeat of the abstract spatial pattern (the same in identity-same and identity-shift conditions) or a repeat of the identical locations of the stimuli (different in the identity-same and shift conditions),

In line with all the previous experiments, the probability of having a response repetition was still lower than having to press a different response key, and the relative probabilities of the different types of response repetition are given in Table 6.

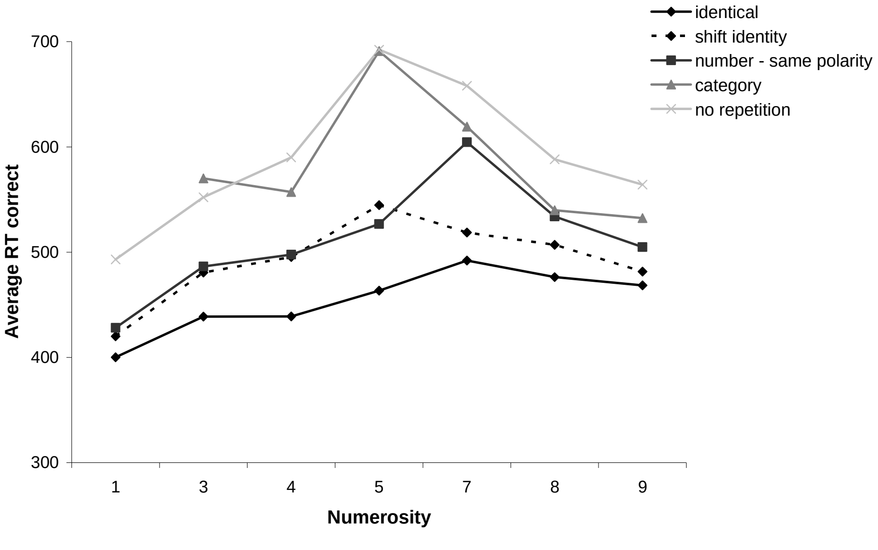
Table 6. Probabilities of repetition types in Experiment 5.3c.

Condition	Random selection	Paired trial	Overall Probability
Identical repetition	0	2/11	0.09
Shifted pattern	0	2/11	0.09
Number repetition	1/9	1/11	0.1
Category repetition	1/3	1/11	0.2
No response repetition	2/3	5/11	0.56

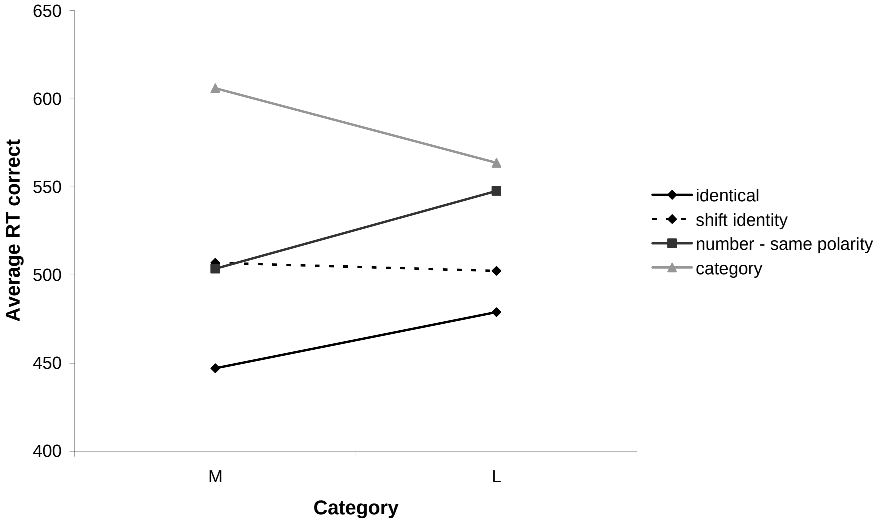
Sixteen participants from the University of Birmingham took part voluntarily for research credits. Each completed the experiment in approximately 60 minutes and received a total of 2880 trials.

Results

The data were pre-processed as before. The effects of the response categories, the repetition types (exact, shifted pattern, number and category) and the numerosities were compared in a within subjects 2 x 4 x 3 ANOVA. Two participants were excluded from the analysis, because they did not reach appropriate levels of accuracy (<60 % of the trials correct). The mean correct RTs are given in Figure 43. There were significant main effects of response repetition (F(3,39)= 56.996, p<.001, partial η^2= .814) and numerosity (F(2,26)= 9.513, p= .001, partial η^2= .423), but no overall difference between RTs on the smaller or the larger numerosities (F(1,13)= .210., p= .654, partial η^2= .016). There were reliable interactions between the two response categories and the repetition types (F(3,39)= 23.098, p< .001, partial η^2= .640), response category and numerosity (F(2,26)= 59.247, p< .001,partial η^2= .820), repetition type and numerosity (F(6,78)= 4.422, p= .008, partial η^2= .254) as well as a significant 3-way interaction (F(6,78)= 6.341, p= .001, partial η^2= .328).



(a)



(b)

Figure 43. RTs on correct responses in Experiment 5.3c. (a) Data depicted as a function of all the numerosities for each response category and repetition type; (b) Data for the repetition effects within each response category, averaged over the constituting numerosities.

The 3 way interaction was further investigated by assessing the effects of the different types of repetition and numerosity within each response category. For the smaller numbers (‘Medium’ category) there were significant main effects of the different repetition types (F(3,39)= 57.273, p<.001, partial η^2= .815) and numerosity (F(2,26)= 32.988, p<.001, partial η^2= .717) as well as a reliable interaction between numerosity and repetition type (F(6,78)= 7.616, p= .001, partial η^2= .369). Category repetitions were slower than number repetitions (F(1,13)= 61.435, p< .001, partial η^2= .825). There was no difference between the number repetition and shifted pattern repetition trials (F(1,13)= .317, p=.583, partial η^2= .024) though identical repetitions were faster than identical shifted stimuli (F(1,13)= 63.038, p<.001, partial η^2= .829). Irrespective of the repetition type, RTs tended to increase as numerosities increased, 3<5 (F(1,13)= 55.460, p< .001, partial η^2= .810) and 4<5 (F(1,13)= 33.314, p< .001, partial η^2= .719) (but 3 = 4; F(1,13)= .215, p= .651, partial η^2= .016). The interaction between repetition type and numerosity for the medium category was eliminated when the category repetition condition was left out (F(4,52)= 2.371, p= .083, partial η^2= .154), suggesting that RTs in this category repetition condition were particularly slowed for numerosity 5.

For the Large category there were significant main effects of the different repetition types (F(3,39)= 32.846, p< .001, partial η^2= .716) and of numerosity (F(2,26)= 39.314, p< .001, partial η^2= .751) and a reliable repetition x numerosity interaction (F(6,78)= 3.490, p= .018, partial η^2= .212). Across the larger numerosities, correct responses to identical repetition trials were faster than shifted identity trials (F(1,13)= 8.675, p= .011, partial η^2= .400), which were in turn faster than number repetitions (F(1,13)= 22.489, p<.001, partial η^2= .634), which in turn again were faster than category repetitions (F(1,13)= 8.087, p=.014, partial η^2= .383). For the larger category RTs decreased as the numbers increased: 7 > 9 (F(1,13)= 50.504, p< .001, partial η^2= .795), 7 > 8 (F(1,13)= 55.930, p<.001, partial η^2= .811) and 8 > 9 (F(1,13)= 6.866, p= .021, partial η^2= .346). The interaction between repetition type and numerosity, for the large response category, was because the difference between the same identity and identity shift conditions, relative to the number and category repetition conditions, tended to increase at numerosity 7.

The critical predictions for the similarity account concern the relations between the same number and category repetition conditions here, since the rating data indicated that participants judged same number displays to be more similar, but this held across the small and larger numerosities alike. When just these critical repetition conditions were considered, then there was a reliable interaction with response category (F(1,13)= 38.680, p<.001, partial η^2= .748). This took the same form as in all of the other experiments. The difference between same number and category repetition trials was greater for small than for the larger displays. This difference was not evident in the rating data.

Discussion

Experiment 5.3c provided new data on (i) the contrast between number and category repetition effects with same polarity displays, and (ii) performance in the same identity condition (in the contrast between same identity and identity shift trials). The results indicated that there was an overall advantage for same identity over identity shift trials, indicating an effect of maintaining the absolute locations of elements across trials, and thus a contribution from low-level similarity effects to performance. In addition, however, there remained an advantage for the identity shift over the same number condition for larger display sizes, while this was completely eliminated for the smaller display sizes. This pattern of results is interesting because the pattern recognition account proposes that the patterns associated with larger display sizes are less discriminable than the patterns associated with smaller display sizes. It should be expected, therefore, that the contribution of a pattern recognition process should be stronger at small than large display sizes. Contrary to this, the data show a contribution of pattern recognition at the larger display size (identity shift < same number trials), which is not present at the smaller display sizes (identity shift = same number trials). This is difficult to account for. On the other hand, if there is a contribution from a subitization process on same number trials with small displays, then this may enable RTs to approach those when pattern identity is maintained, as was observed.

Along with this last result, the data also indicate that the benefit for same number over category repeat trials was greater for small than for larger display sizes. Given that any differences in the similarity ratings across these repetition conditions were equal for the display sizes (Experiment 5.3a), then this again seems difficult to explain in terms of pattern recognition. The result is consistent with the subitization account, however, if subitization of the same number value facilitates performance for small but not for larger displays.

Experiment 5.4: Controlling for visual similarities and luminosity

In the final experiment, the effects of pattern/location, number and category repetitions were again examined, but two further changes were added: (i) the overall luminosities of the displays were controlled, which eliminated luminosity changes as a potential cue that could be used to judge numerosity; and (ii) the categories were re-defined so that the perceivable difference between each pair of numerosities within the response category was the same for the numerosities in the smaller number category and for those in the larger number category (following Weber's Law). It was possible that differential repetition effects were reduced for the larger display sizes in the earlier experiments because luminosity was used as a cue to magnitude (though see Experiments 5.3b and c) and because the different numerosities within the Large category were more difficult to discriminate from each other than the smaller numerosities.

Method

Stimuli

The numerosities we used were 2,3,4 in one category and 6,8 and 11 in the other category. They are considered to be "visually discriminable" numbers, when a Weber discriminability ratio of between 0.75 and 0.80 is assumed (see also Shuman & Kanwisher, 2004). The ratio between the consecutive numerosities was kept constant, therefore creating equally visually discriminable numerosity displays.

The displays contained 2 to 11 dots presented on a grey background (RGB: 127,127,127). The dots were made by combining binary noise with a circular gaussian envelope. The diameter of each dot was 30 pixels, on a screen with 1280 x 1024 pixel resolution. The dots were drawn randomly in the centre of the display, within a 450x450 pixel window, with the constraint of a minimum interdot distance and distance from the fixation cross of 30 pixels.

In order to avoid systematic variation of the numerosity with the luminosity of the displays, the displays were manipulated as follows. For each display the dots were randomly sampled (with replacement) from a list of 10 elements. These 10 elements were measured by a Minolta LS110 light meter, to fall within a range of 1 cd/m^2 from the average background luminosity. The luminosity of the background measured 12.2 cd/m^2, the dots in the list were chosen so that there were 4 items ‘darker’ than the background with luminosity values: 11.2 cd/m^2, 11.7; two similar to the background: cd/m^2, 12.2 cd/m^2, and four with brighter luminosity than the background: 12.7 cd/m^2, 13.2 cd/m^2. These values were measured on a high resolution CRT monitor in a completely darkened room.

By sampling the elements in this way, luminosity was not the same in each display, across all numerosities. Instead, this method eliminates the possibility of there being a consistent relationship in which larger displays always have a larger luminosity than smaller displays (e.g. it is possible that a display numerosity 8 could be ‘lighter’ or ‘darker’ than a display with numerosity 2), and on average, the luminosity was the same across the number conditions. For an example of the stimuli used, see Figure 44.

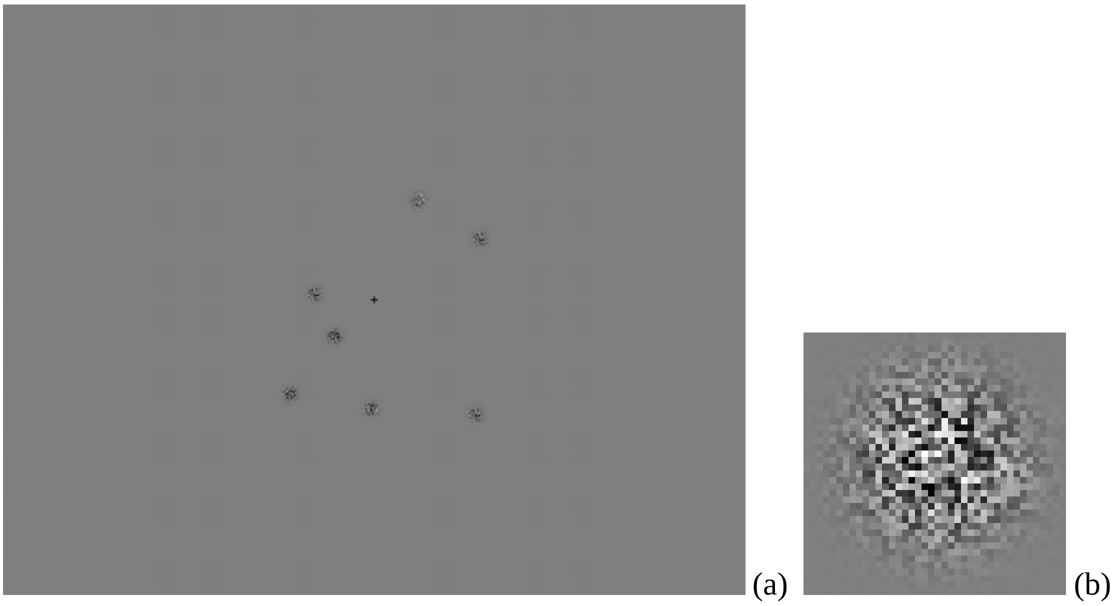


Figure 44. (a) Example stimulus used in Experiment 5.4. (b) Close up of a single dot.

Procedure

The procedure was the same as in all the previous experiments, except that there were only 2 response categories: “Small” and “Large”. The participants’ task was to estimate the category to which the displays belonged as accurately and as fast as possible. Participants responded “small” (key 1 on the numeric pad) when there were fewer than 5 dots in the display and “large” (key 2 on the numeric pad) when there were more than 5 dots present.

Design

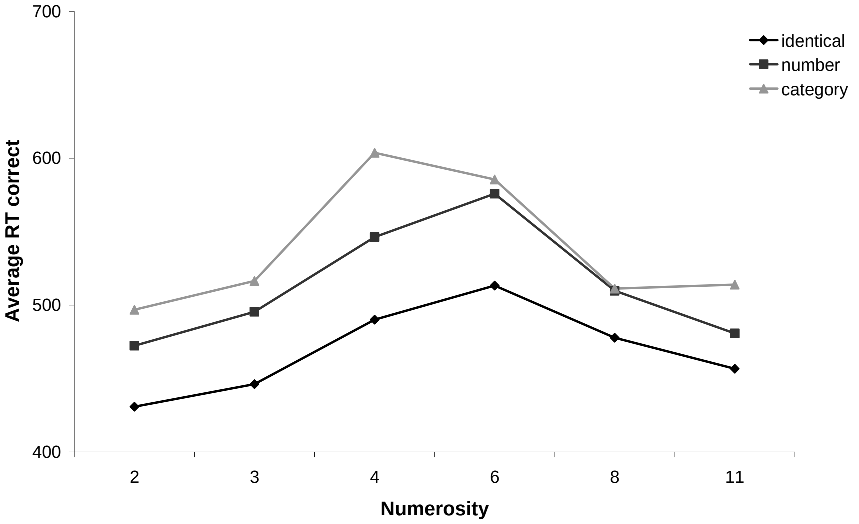
The trial sequence was manipulated in order to introduce different kinds of repetition. A *category repetition* was a repetition of the required category response, with a different numerosity. A *number repetition* consisted of a re-sampling of the dots from the list as well as a re-randomisation of the dots’ locations. On *identical repetition* trials, there was a re-sampling of the dots, but the spatial pattern was kept the same.

The occurrence of the 2 response categories (Small and Large) was evenly distributed across the trials. The repetition manipulation was added by making a pseudo-random list of conditions. This was done in order to eliminate the previous deleting of trials that were 2nd order repetitions. It also ensured a fixed number of trials per condition (16 trials for each numerosity for identical, number and category repetitions, and 107 trials for each numerosity where there was no repetition of the response category).

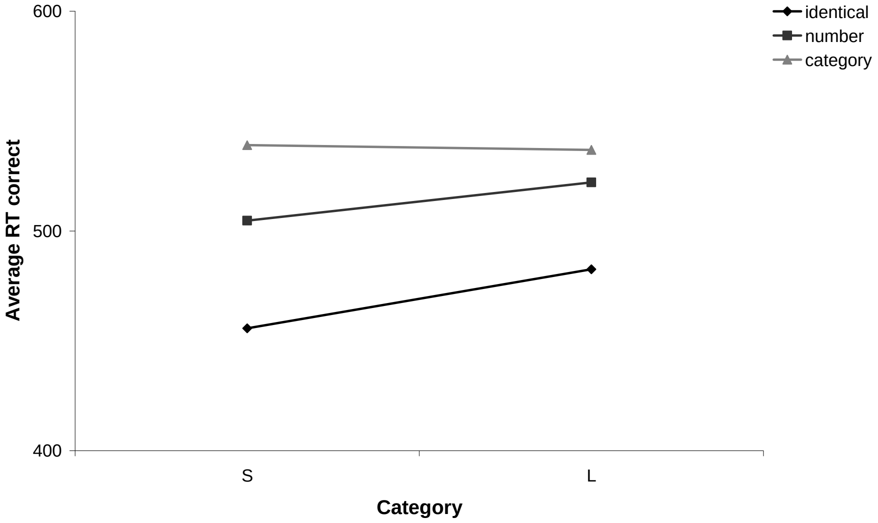
Sixteen participants from the University of Birmingham took part voluntarily for research credits. They received a total of 786 trials divided over six blocks with breaks after each block.

Results

Outliers which were more than 3 standard deviations from the mean were excluded from the analysis. The effects of the response categories, the repetition types (identical, number and category) and the numerosities were compared in a within subjects 2 x 3 x 3 ANOVA. The correct RTs are presented in Figure 45. There were significant overall effects of response repetition ($F(2,30)$= 91.596, $p<$ .001, partial η^2= .859), as well as overall effects of the different numerosities within each category ($F(2,30)$= 13.660, $p<$ .001, partial η^2= .477), but no overall effect of the response category ($F(1,15)$= 2.557, p= .131, partial η^2= .146). There were reliable interactions between response category and numerosity ($F(2,30)$= 92.726, $p<$.001, partial η^2= .861), repetition type and response category ($F(2,30)$= 10.196, p= .001, partial η^2= .405), and repetition types and numerosity ($F(4,60)$= 5.727, p= .003, partial η^2= .276), and there was also a reliable 3 way interaction: repetition type, numerosity x response category ($F(4,60)$= 2.971, p= .042, partial η^2= .165).



(a)



(b)

Figure 45. RTs (ms) on correct responses in Experiment 5.4. (a) RTs for each numerosity and repetition type for the small and large response categories. (b) RTs for each repetition type and each response category.

In the Small response category there were significant main effects of repetition (F(2,30)= 68.109, p<.001, partial η^2= .820) and numerosity (F(2,30)= 62.954, p< .001, partial η^2=.808) and a reliable interaction (F(4,60)= 5.426, p= .006, partial η^2= .266). Overall, RTs were faster with identical repetitions than with category repetitions (F(1,15)= 110.308, p< .001, partial η^2= .880), and number repetitions (F(1,15)= 59.214, p<.001, partial η^2= .798). Crucially, as before, number repetitions were faster than category repetitions (F(1,15)= 23.762, p< .001, partial η^2= .613). The interaction arose because these differential priming effects were larger for display size 4 than for the other small display sizes. However, omitting display size 4 still gave raise to a main effect of repetition type (F(2,30)= 73.954, p< .001, partial η^2= .831) while the interaction between numerosity and repetition type disappeared (F(2,30)= 1.417, p= .258, partial η^2= .086).

In the Large response category, there also was a significant main effect of repetition type (F(2,30)= 59.863, p< .001, partial η^2= .800) and of numerosity (F(2,30)= 64.696, p< .001, partial η^2= .812), and a reliable interaction (F(4,60)= 3.030, p= .044, partial η^2= .168). Overall there were reliable differences between category and identical repetitions (F(1,15)= 119.455, p< .001, partial η^2=.888), category and number repetitions (F(1,15)= 8.587, p= .010, partial η^2=.364), and number and identical repetitions (F(1,15)= 48.281, p< .001, partial η^2= .763). RTs in the Large response category decreased as numerosity increased, 6>11 (F(1,15)= 79.655, p< .001, partial η^2= .842), 6>8 (F(1,15)= 61.702, p< .001, partial η^2= .804), and 8>11 (F(1,15)= 14.486, p= .002, partial η^2= .491). The repetition type x numerosity interaction seems to reflect the divergence between the category and number repetitions at numerosity 11.

Although both the Small and Large response categories showed differences between number and category repetition conditions, this difference was significantly larger in the Small response category, as demonstrated by a significant interaction between the response categories and the repetition type, when only number and category repetitions were entered in the analysis (F(1,15)= 6.625, p= .021, partial η^2= .306).

Discussion

Although Experiment 5.4 took measures to ensure that overall luminance was not correlated with number, and that numbers within the small and large response categories were equally visually discriminable, much the same pattern of results occurred as before. In particular, for the smaller display sizes (the small response category here), category repetitions were slowed relative to number repetition trials, while there was also an advantage for keeping the items in the same location. The contrast between category and number repetition did emerge here for the large response category too. This is suggestive either of of participants being sensitive to exact number even with the larger numerosities, provided the items within the common response category are sufficiently discriminable, or the more discriminable differences in overall pattern influencing performance. However, even with highly discriminable larger numbers, the effects are smaller than with smaller, subitizable numbers. This supports the idea that similarity alone cannot account for our results in this and also the previous experiments. A more consistent account is that access to exact number identity emerges more rapidly with smaller numbers, facilitating performance when that access process is repeated (number repeat trials) and disrupting it when visually discriminably different numbers must be assigned to the same response category (on category repeat trials with small displays).

General Discussion

As noted in the Introduction, there has been a long-standing debate about whether visual arrays of up to 4 or so items can be rapidly assimilated using processes distinct from other enumeration operations. This issue was examined indirectly here, by assessing priming effects in a number estimation task. Performance was contrasted when consecutive displays were identical, maintained their pattern but shifted position, had the same number but changed patterns, and had different numbers but were assigned to the same response category. Across the experiments a highly consistent pattern of results emerged:

1. For displays with up to 5 items there was a clear drop in performance when items repeated from the same response category relative to when displays repeated with the same number. This result was much less evident with larger display sizes, and emerged only when the items within the large display sizes are made highly discriminable, and even then it remained a much smaller effect (Experiment 5.4).
2. There were benefits from repeating the same patterns in the same locations, and this occurred for both small and larger numerosities. For small numerosities, this effect seems largely to be based on consecutive displays having items in the same locations (Experiment 5.3c). For these subitizable numerosities there was no added benefit from keeping the pattern and shifting its location compared with presenting a completely different pattern (in the number repeat condition). For larger numerosities, there was some added benefit from repeating the same pattern, suggesting some sensitivity to the overall pattern in this case.

The contrasting results with small and large display sizes arose even though the experiments controlled for display area, inter-item spacing and average luminance.

Two accounts can be put forward to explain these results. The pattern recognition account suggests that visual enumeration can be based on the assimilation of different patterns and relating those patterns to specific numbers (Mandler & Shebo, 1982). As the patterns formed by small numbers are more discriminable than those formed by larger display sizes, the pattern information can be used to support the enumeration of small numbers more than that of larger numbers. This is supported by rating data indicating that the patterns formed by different small displays are more discriminable than those formed by different larger displays (Logan & Zbrodoff, 2003) and by evidence that larger patterns can be enumerated rapidly once canonical patterns are used for large as well as small displays (Mandler & Shebo, 1982; Wolters et al., 1987; Lassaline & Logan, 1993; Palmeri, 1997). To account for the present data, the pattern recognition account must hold that, at small displays, configurations with the same number of items must be more similar than configurations with different numbers of items, and the similarity of same number displays must be higher for small relative to larger display sizes. In addition, the similarity of displays containing different numbers of items but from the same response category here should be low for small displays and relatively high for larger displays (since RTs are then close to those in the other repetition conditions). The similarity rating data supported some but not other aspects of these proposals. Similarity was judged higher for same number than same category displays, but this difference was the same for small and large displays, and similarity ratings for same number and same category displays did not differ when displays had the same contrast polarities. The one exception was that, for small relative to larger display sizes, similarity was judged higher in the same identity condition when the displays differed in contrast polarity. However, this difference in similarity ratings seemed to have no effect on numerosity judgements. RTs in the numerosity judgement task were faster for same identity over same number, different polarity trials, and this advantage did not change across the display sizes.

Could the differences in the results for the rating study and the numerosity judgements reflect different scalings for these measures? For example, the ratings may fail to discriminate differences in similarity in the same number condition for small and large display sizes because all same number comparisons are judged dissimilar, relative to when the patterns were identical. Against this, the ratings in the same number condition were in the middle of the similarity range, and so unlikely to be contaminated by floor or ceiling effects. In addition, differences in the ratings were observed when same number displays changed in contrast polarity (similarity ratings were higher for small than for large display sizes); yet, in this case, the drop in performance relative to the same identity condition (where visual similarity was at maximum) was no greater for large than for small display sizes. Thus there is evidence for no differences in ratings (same number, same polarity) yet a difference in numerosity judgements (same number same polarity vs. the category repeat baseline), and evidence for a difference in ratings (same number, different polarity) but no difference in numerosity judgements (same number different polarity vs. same identity baseline). The data suggest that visual similarity, alone, cannot explain performance in the numerosity judgement task.

There are two other pieces of evidence that run counter to the visual similarity account. One is that even when canonical patterns were used for the larger displays sizes (in Experiment 5.1b), there remained a larger difference between the same number and same category conditions for small than for larger displays. With canonical patterns, the enumeration of larger displays should be based on pattern recognition, similar to the enumeration of small display sizes (Mandler & Shebo, 1982). The second is that even when the display sizes were varied non-linearly, to equate discriminability within the different small number sizes to those within the different larger number sizes (based on Weber's Law), the differential priming result remained (small [same category – same number] > large [same category – same number]; Experiment 5.4).

Nevertheless, Experiment 5.1 did provide evidence for some contribution from pattern recognition to numerosity judgements, because a same identity advantage arose for larger display sizes when canonical patterns were used; this advantage was not present with random displays (Experiments 5.1b vs. 5.1a). Hence there is evidence here for pattern recognition supporting enumeration, but it is arguably not the only factor involved.

The alternative account is that small number displays can be apprehended through independent, parallel processing of their members (subitization), which gives rise to rapid enumeration of small display sizes (Trick & Pylyshyn, 1993). According to this account, the differential priming for small over large displays, in the same number compared with the same category condition, reflects (i) the apprehension of the same subitized value across same number trials, and (ii) the apprehension of different exact numbers in the repeat category condition. Since this subitization process only operates successfully for small display sizes, the differential priming effect emerges only for displays of 5 items or less. For larger display sizes, numerosity judgements will be based on an estimated value. Since this value is approximate, rather than exact, then it operates across all the repetition conditions for larger display sizes, equating performance (see Experiment 5.1a). The present results also suggest that the apprehension of different small numbers, in the same category condition, appears to be automatic. Performance in this condition, for small number displays, was relatively slow in all of the current numerosity experiments, and sometimes as slow as when the response category changed across trials (the no repetition condition). It appears that participants could not help but detect the differences in small number values in this case. On top of this, though, the evidence presented here indicates that there can be a pattern recognition process which contributes to numerosity judgements, which is responsible for the strongest carry-over effects in the same identity condition. The effects of pattern similarity are based both on elements maintaining their locations across consecutive displays and on the same spatial configuration being maintained (see Experiment 5.3b, Figure 42).

One other reason to argue for there being a process of small number assimilation, separate from pattern recognition, comes from neuropsychology. Patients with bilateral damage to the posterior parietal cortex are notoriously poor at enumeration (Dehaene &

Cohen, 1994; Humphreys, 1998). In patient GK (Demeyere & Humphreys, 2007), the ability to count even small numbers of items was extremely impaired. Despite this, GK was able to recognise many simple patterns, including schematic faces made up of elements like the ones used here, in a holistic fashion (Shalev & Humphreys, 2002). Thus the recognition of simple patterns was relatively spared. If he was able to use this relatively spared pattern recognition process to count, then he should have been able to count small numbers – especially as proponents of pattern recognition in counting argue that small numbers of objects can always be identified as a canonical form (e.g. Mandler & Shebo, 1982). These neuropsychological results suggest that this was not the case.

In conclusion, the results indicate that the rapid assimilation of small exact numbers appears to involve two processes: the recognition of familiar patterns and the parallel assimilation of the stimuli (subitization). These processes are distinct from magnitude estimation, which occurs with larger displays, and generates approximate rather than exact number representations. The distinction between exact representation of small numbers, and approximate representations of larger numbers, supports the argument for different numerical systems for enumeration and estimation (Feigenson et al., 2004)

Table 7. Overview of accuracy performance: Mean proportions of errors for the 4 reported Experiments.

		Exp 5.1a: random		Exp 5.1b: canonical		Exp 5.2a: display area		Exp 5.2b: middle category		Exp 5.3 b- changing polarities		Exp 5.3c: shifted identity		Exp 5.4: Weber fractions	
Repetition	Category	Num.	Prop Error	Num.	Prop Error	Num.	Prop Error	Num.	Prop Error	Num.	Prop Error	Num.	Prop Error	Num.	Prop Error
Identical	S							2	0.007						
Identical	S							3	0.031						
Identical	S	1	0.020	1	0.024	1	0.008	4	0.060	1	0.011	1	0.004		
Identical	M	3	0.033	3	0.016	3	0.029	6	0.035	3	0.028	3	0.018	2	0.022
Identical	M	4	0.031	4	0.027	4	0.007	7	0.015	4	0.009	4	0.017	3	0.027
Identical	M	5	0.024	5	0.053	5	0.015	8	0.026	5	0.044	5	0.028	4	0.045
Identical	L	7	0.036	7	0.037	7	0.080	15	0.048	7	0.063	7	0.070	6	0.054
Identical	L	8	0.019	8	0.064	8	0.033	16	0.030	8	0.030	8	0.051	8	0.040
Identical	L	9	0.025	9	0.041	9	0.047	17	0.041	9	0.032	9	0.037	11	0.027
Shift identity	S							2	-						
Shift identity	S							3	-						
Shift identity	S	1	-	1	-	1	-	4	-	1	-	1	0.017		
Shift identity	M	3	-	3	-	3	-	6	-	3	-	3	0.032	2	-
Shift identity	M	4	-	4	-	4	-	7	-	4	-	4	0.014	3	-
Shift identity	M	5	-	5	-	5	-	8	-	5	-	5	0.053	4	-
Shift identity	L	7	-	7	-	7	-	15	-	7	-	7	0.050	6	-
Shift identity	L	8	-	8	-	8	-	16	-	8	-	8	0.007	8	-
Shift identity	L	9	-	9	-	9	-	17	-	9	-	9	0.026	11	-
Number	S							2	0.030						
Number	S							3	0.030						
Number	S	1	0.023	1	0.045	1	0.025	4	0.072	1	0.019	1	0.014		
Number	M	3	0.022	3	0.044	3	0.020	6	0.044	3	0.037	3	0.027	2	0.058
Number	M	4	0.025	4	0.034	4	0.004	7	0.028	4	0.016	4	0.018	3	0.071
Number	M	5	0.033	5	0.041	5	0.024	8	0.064	5	0.034	5	0.040	4	0.071
Number	L	7	0.061	7	0.107	7	0.043	15	0.042	7	0.078	7	0.086	6	0.107
Number	L	8	0.030	8	0.064	8	0.027	16	0.034	8	0.036	8	0.025	8	0.049
Number	L	9	0.036	9	0.061	9	0.017	17	0.018	9	0.035	9	0.026	11	0.027

Category	S							2	0.019						
Category	S							3	0.070						
Category	S	1		1		1		4	0.208	1		1			
Category	M	3	0.062	3	0.110	3	0.054	6	0.030	3	0.043	3	0.065	2	0.049
Category	M	4	0.050	4	0.055	4	0.021	7	0.019	4	0.029	4	0.037	3	0.107
Category	M	5	0.115	5	0.166	5	0.080	8	0.051	5	0.116	5	0.135	4	0.214
Category	L	7	0.052	7	0.094	7	0.061	15	0.056	7	0.177	7	0.104	6	0.125
Category	L	8	0.035	8	0.072	8	0.030	16	0.038	8	0.081	8	0.035	8	0.067
Category	L	9	0.041	9	0.081	9	0.026	17	0.052	9	0.046	9	0.027	11	0.054
No repetition	S							2	0.017						
No repetition	S							3	0.040						
No repetition	S	1	0.038	1	0.058	1	0.031	4	0.130	1	0.053	1	0.040		
No repetition	M	3	0.056	3	0.062	3	0.038	6	0.064	3	0.044	3	0.041	2	0.014
No repetition	M	4	0.052	4	0.064	4	0.024	7	0.070	4	0.053	4	0.037	3	0.018
No repetition	M	5	0.130	5	0.158	5	0.087	8	0.105	5	0.159	5	0.131	4	0.072
No repetition	L	7	0.113	7	0.113	7	0.108	15	0.077	7	0.126	7	0.110	6	0.050
No repetition	L	8	0.063	8	0.059	8	0.055	16	0.062	8	0.079	8	0.055	8	0.014
No repetition	L	9	0.040	9	0.068	9	0.037	17	0.054	9	0.055	9	0.044	11	0.011

CHAPTER 6:

SUBITIZING IS SPECIAL: EVIDENCE FOR THE EXACT REPRESENTATION OF SMALL NON-SYMBOLIC NUMBERS

Synopsis

An fMRI pair-adaptation paradigm was used to identify the brain regions linked to exact apprehension of non-symbolic small numbers (subitizing). Participants classified stimuli on the basis of their numerosities (fewer or more than five dots). Repetition of the same small number, in a different pattern, elicited markedly more neuronal adaptation in the (left) intra-parietal sulcus (IPS) than repeated stimuli with different numbers, but from the same response category. In contrast, repetitions of the same larger numerosity did not elicit any number-specific adaptation. The effects cannot be attributed to differences in visual discriminability across the small and larger numerosities. The data suggest that the left IPS adapts to repetition of small exact non-symbolic numerosities irrespective of their shape, consistent with this being the site of visual small number apprehension. We propose that small non-symbolic numerosities are represented exactly, in an abstract manner, in the left IPS.

Introduction

It has long been known that our ability to enumerate visually presented stimuli varies with the number of items present (see Chapter 1 Introduction). The enumeration of small numbers (1-4) is near perfect and proceeds rapidly; whereas for larger displays there are substantial increases in RTs and errors per extra item that needs to be counted (Mandler & Shebo, 1982; Trick & Pylyshyn, 1993). This contrast, between efficient enumeration of small numbers, and less efficient enumeration of larger numbers, has led to some researchers arguing for distinct processes being involved in these two instances: a parallel subitization process and a serial counting process. Others disagree and a debate about whether subitizing is special and can be differentiated from counting is still ongoing (see Chapter 1 Introduction).

fMRI adaptation & nonsymbolic quantity processing

fMRI adaptation takes place when the neural response decreases when a stimulus is repeated (Grill-Spector et al., 1999; Kourtzi & Kanwisher, 2001). Brain areas showing adaptation in the face of a change in a stimulus or a response reflect a stimulus or response code that is invariant to the change. Consequently, fMRI adaptation can be used as a probe to measure brain areas that are (showing adaptation) or are not (showing release from adaptation) invariant to a given change. fMRI adaptation has previously been used in many studies of number processing, and tasks involving symbolic numbers (such as mental arithmetic and number comparisons) have indicated the involvement of the IPS in abstract number representation (for a review, see Dehaene et al., 2003). However, whether or not this specialized number area also extends to non-symbolic magnitude processing remains unclear.

Piazza et al. (2004) first demonstrated fMRI adaptation in the IPS during passive viewing of sets of a fixed quantity of dots (16). They found there was a marked recovery of the fMRI response in bilateral intraparietal sulci when a number-deviant stimulus appeared, compared to a stimulus that differed in local shape from the habituated stimuli. Moreover, recovery of the fMRI signal was related to the distance between the number-deviant and the adapted number - the larger the difference, the stronger the recovery effect.

Cantlon et al. (2006) used a blocked adaptation design, where a stream of visual arrays was presented containing the same number of elements (either 16 or 32) and the same local shape element (circles). They assessed recovery of adaptation to a deviant stimulus in which either the local shapes differed (squares to circles or vice versa), or a different number of elements were presented (half or double the adapted number). They found that the IPS showed a greater response recovery from adaptation to number deviants than to shape deviants (cf. Piazza et al., 2004).

In contrast to the above results, Shuman & Kanwisher (2004) found no adaptation effect for passive viewing of non-symbolic quantities. They presented subjects with blocks of stimuli that were either constant or randomly varying in each of two dimensions: the number of elements and the local shape of the elements. They found no significant number adaptation effects in the IPS or any other region previously implicated in number processing. In another experiment they compared a colour judgement task with a number judgement task made to the same displays and found no activations of the number task over the colour judgements in the IPS. One possible explanation here is that only symbolic number is represented and processed in the putative parietal number area. The authors also suggest that it is possible that the IPS *is* involved in number representation and processing but it is also involved in many other processes that do not involve number or even continuous magnitude or in other words, number processing may be localized to some degree in the IPS, but the IPS is not domain-specific for number.

Piazza et al. (2007) subsequently had participants passively view a series of dot patterns and symbolic numbers. They found adaptation in bilateral IPS when participants saw approximations of the same number, compared to when different numbers were presented, and this was independent of whether there was a change in notation (from dot pattern to symbolic and vice versa). In this case, the IPS showed recovery from adaptation to the same degree when a deviant symbolic number was presented amongst a stream of constant non-symbolic quantities, compared to when a deviant non-symbolic number was presented amongst a stream of constant symbolic quantities. This suggests that the IPS may contain representations that respond to an abstract number irrespective of how it is presented. However, it should be noted that only 2 categories were employed (≈20 and ≈50) and participants were informed of the number of dots that could appear. Consequently it is plausible that participants automatically coded the non-symbolic numerosities in symbolic terms (e.g., ‘20’ vs. ‘50’). This would automatically give rise to adaptation to the same abstract number whether participants viewed dot patterns or Arabic numerals.

The neural correlate of subitizing

In none of the above studies was a distinction made between small subitizable numbers and larger numerosities. Studies specifically concerned with subitizing traditionally contrast subitizing with counting (e.g. Sathian et al., 1999; Piazza et al., 2002; Piazza et al., 2003, see Chapter 1 Introduction). In these studies, no specific areas for subitizing have been identified: instead, all areas active in subitizing are also activated to at least the same degree in counting. Since counting involves more mental processes than subitizing (e.g., individuating and localizing the items, switching attention, inhibiting ‘re-counting’), then the greater activation for counting is not surprising, especially when a technique that might provide finer-grained localisation, such as adaptation, is not employed. One study reporting regions showing greater activation for subitizable over non-subitizable numbers has been reported by Ansari et al. (2007). These authors used dot patterns in a number comparison task, where 2 patterns were presented sequentially. Participants pressed one button if the first array was numerically larger than the second, and another if the second display was numerically larger. They found greater activation for small compared with larger number comparisons in the right temporo-parietal junction and greater activation for large than small number comparisons in the calcarine and parieto-occipital sulci. In addition, activation in the TPJ was suppressed relative to baseline in the large numerosity condition. The authors explain these results in terms of the stimulus-driven “bottom-up” attention being linked to subitizing and goal driven, “top-down” attention being linked to larger number processing. In addition, conjunction analyses for small and large number processing strongly implicated bilateral regions of the IPS.

Hyde and Spelke (2009) also compared the processing of small quantities of dots (1-3) to larger numerical quantities (8-24) outside of an enumeration paradigm, by measuring event-related potentials to the same or a different number of dots in a passive viewing adaptation paradigm. They found that an early-evoked component (N1), observed over widespread posterior scalp locations, was modulated by absolute number with small, but not large, number arrays. In contrast, a later component (P2p), observed over the same scalp locations, was modulated by the ratio difference between arrays for large, but not small, numbers. This fits with Feigenson et al.’s proposal of two separate core systems of number, one concerned with exact number representation and the other with approximate (estimated) number representation (Feigenson et al., 2004)

Here fMRI adaptation was used as an indirect way of assessing subitizing activity in a number estimation task where participants were asked to judge whether the number of items was greater (classified as ‘Large’) or smaller than 5 (classified as ‘Small’). The behavioural studies conducted in Chapter 5 suggest that specific forms of repetition effect occur with small (subitizable) and large (estimate only) numbers. In particular, the contrast between performance when the same number of items is presented, compared with when the number differs, is greater for small numbers (e.g., a display of 3 items followed by one of 4) than for larger numbers (a display of 6 items followed by one of 8). This occurred even though, in the estimation task, the same response occurred across both sets of consecutive trial (i.e. both ‘small’ or both ‘large’). This differential repetition effect was attributed to (i) the same subitization process being repeated for the same small numbers leading to an automatic exact small number representation and a different exact small number representation arising from a subsequent different small number, and (ii) the same estimation process being involved for larger numbers irrespective of whether there is the same or a different number of items across consecutive trials. These effects held even when estimation decisions could not be based on factors such as overall brightness, the area covered by patterns or the similarity of the patterns on number repeat trials.

The present study exploited these differential repetition effects to examine whether, relative to the repetition conditions, there were brain regions that showed a greater recovery of activation when one small number followed another different small number, compared with when one larger number followed a different larger number. Since, in all of these conditions, the same response (consecutive displays categorized as both ‘Small’ or both ‘Large’) would be involved across trials, any differential adaptation effects should not emerge in response selection and execution.

Method

Subjects

Twelve healthy subjects (3 males and 9 females, mean age: 26 years; range 20-34), all but two right handed, gave written informed consent according to ethical procedures of the Birmingham University Imaging Centre (BUIC). None of the participants had previous neurological or psychiatric symptoms and all had normal or corrected vision.

Stimuli

The numerosities presented in the “Small” category were 2, 3, 4 while they were 6, 8 and 11 in the “Large” category. These quantities represent “visually discriminable” numbers with a Weber discriminability ratio of between 0.75 and 0.80 (see also Shuman & Kanwisher, 2004). Each stimulus was presented on a screen situated outside the scanner and projected onto a mirror 30 cm above participants, subtending a visual angle of $\approx$ 10°. The displays were presented on a grey background. The dots were randomly positioned around the centre of the screen, along with an always present fixation cross. Apart from this, the displays used were the same as in Experiment 5.4 – see Figure 44 - with no consistent relationship between numerosity and luminosity.

Design

There were 4 types of repetition condition. In the *no repetition* condition, consecutive displays were drawn from the different response categories (Small then Large, or Large then Small). There were a further 3 conditions where the response was repeated across trials. On *identical repetition* trials, exactly the same pattern and same number of elements repeated across trials. On *number repetition* trials the pattern changed but the same number of dots appeared on consecutive trials. In the *category repetition* condition, the numbers of dots on consecutive trials were either both small or both large, but in each case the displays contained different numerosities. See Figure 46 for an overview of the design and procedure of the experiment.

We asked participants to mentally assign the displays to their respective categories (<5 “Small”, >5 “Large”). For the majority of the trials, no explicit response was required; however, on occasional trials subjects were cued (with a red number 1 or 2, after the paired numerals) to respond with a key press to the category that the first or the second display belonged to. These catch trials were modelled separately in the analysis, so as not to confound any resulting activation with response selection.

The stimuli were presented in 8 blocks, each containing 73 paired presentations (6 identical, 6 number and 6 category repetitions per category - 2 for each numerosity - and 30 no repetition (different category) trials). Each block contained 7 catch trials to ensure the participants were paying attention and were performing the task at hand (mentally categorizing the displays into ‘Large’ or ‘Small’ categories).

Procedure

We used an event-related jittered design, in which one event consisted of a paired presentation of two numerosity stimuli (in a similar procedure to Kadosh, Kadosh, Kaas, Henik, & Goebel, 2007). Each block started with a 20 sec fixation period to allow for T1 equilibration. Next, the paired numerosity displays were presented, each for 400 ms with a 500 ms fixation interval. This was followed by a jittered period of fixation for 3000- 5000 ms. (averaging out at 4000 ms over the block). On approximately 10% of the trials (7/73) a response was required. These sparse response trials occurred in pseudo-random positions throughout the block, after a paired display. On these trials a cue (a red number 1 or 2) appeared 500 ms after the 2nd member of the pair. The task was to respond whether the number of dots in the cued numerosity display was less than or greater than 5. The cue remained on screen for 1000 ms and was followed by a fixation period of 2500 ms. The key-presses and reaction times to these trials were recorded. Figure 46 illustrates the sequence of events on a trial.

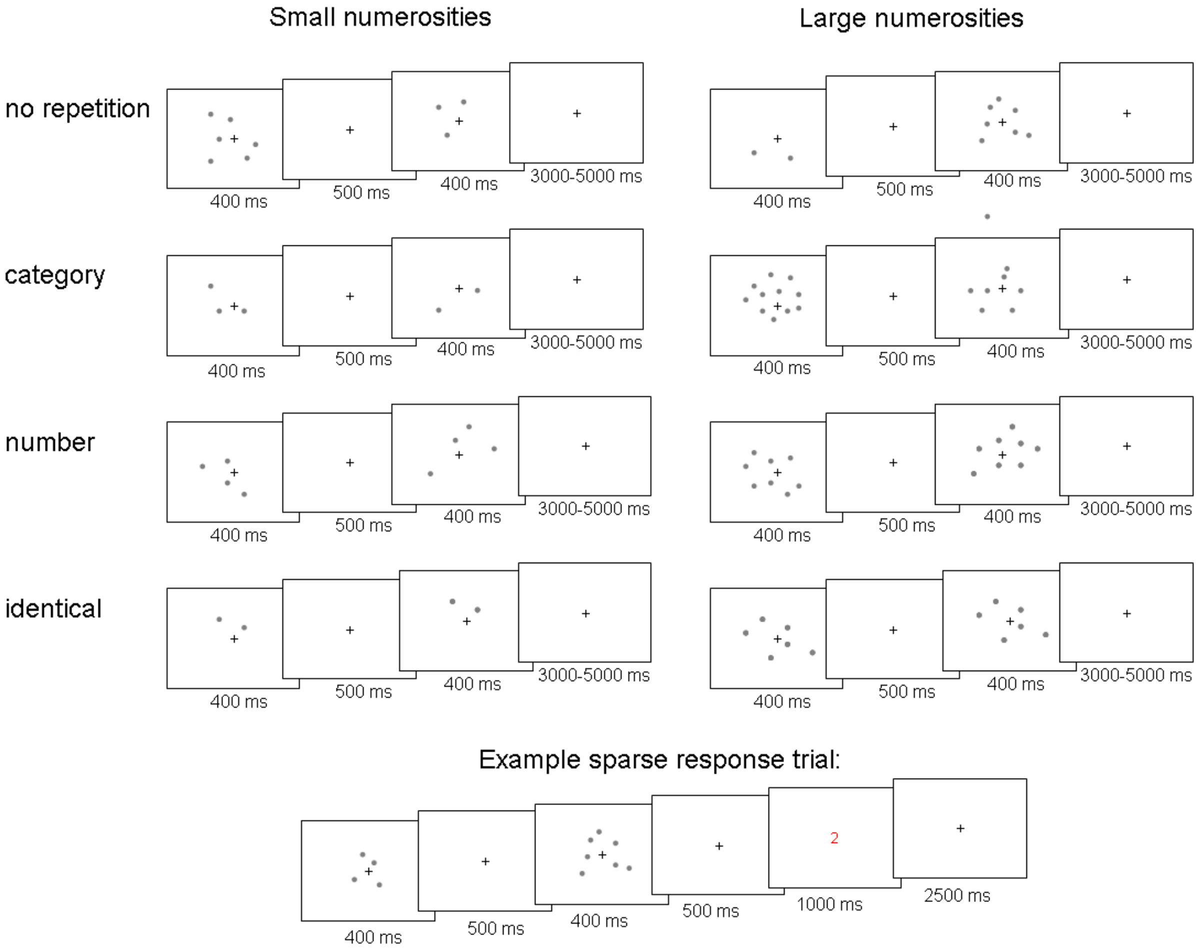


Figure 46. Illustration of the sequence of events containing examples of the different repetition conditions for small and larger numerosities. In addition, an example of the sequence of events on a sparse response trial

Instructions

The participants were instructed to watch the presentations and mentally categorize both items in the paired displays as Small (< 5) or Large (>5). Participants were told that the task required the report of one of the images after the occasional cue occurred (display one or two after the cue ‘1’ or ‘2’). To carry out this task they were told to try and mentally categorize each image. The response categories were clearly assigned, and, for trials when a response was required, the right index finger button was assigned to numerosities belonging to the “Small” (<5) category, and the right middle finger button to numerosities belonging to the “Large” (>5) category. Scanning was preceded by a practice session to familiarize the participants with the design.

Image acquisition

Imaging was performed by using a 3-Tesla scanner (Achieva Philips) with an eight channel phase array coil. Structural images were acquired with a T1-weighted sequence. Functional images were acquired with a gradient echoplanar T2* sequence by using blood oxygenation level-dependent contrasts. The image matrix was 112x112. Each functional image was composed of 29 slices (2.5mm thickness with a 1.1 – 1.2 mm gap, nominal voxel size 3 x3 x3 mm), positioned to cover most of the brain (with the emphasis on covering the whole of the frontal and parietal lobes). This meant that sometimes the earlier visual areas were not scanned. Repetition time (TR) was 2 sec, TE was 35 msec, and there was a 80° flip angle. A total of 205 functional volumes were acquired continuously in one scanning session. There were 8 functional imaging sessions in total.

Data analysis

The data were analyzed with SPM5 (Wellcome Department of Imaging Neuroscience, London; www.fil.ion.ucl.ac.uk/spm). The first five volumes of images were discarded to allow for T1 equilibration. The remaining 200 (x8 sessions) functional image volumes were realigned to the first image (Ashburner & Friston, 2003) and unwrapped to account for movement by distortion interactions (Andersson, Ashburner, & Friston, 2001), the images were then normalised to the standard MNI space (Ashburner & Friston, 2003). Finally the data were smoothed using 8x 8x 8mm FWHM Gaussian kernel to account for residual inter-subject variability. Individual events were modelled by a canonical synthetic hemodynamic response function (Friston et al., 1998). The analysis was based on two-step summary statistics (Penny et al., 2003a). At the first level, we used the general linear model to generate parameter estimates for event-related activity at each voxel for each subject in response to the presentation of each of the paired-stimulus conditions. Regressors of no interest included the catch-trials, the six movement parameters to correct for residual signal changes due to head movement, and a set of harmonic repressors to model low fluctuation (1/128Hz) in the signal that is typically associated with scanner and biological noise. Consistent effects across subjects were tested in a second level analysis, in which subjects were treated as random variables (Penny et al., 2003b). The analysis focused on comparing repetition effects within the small and large number categories. Based on previous literature, we hypothesised that these comparisons will be associated with responses within occipital-parietal regions, but for completeness we report in the tables cluster larger than 20 voxels at $P < 0.001$ uncorrected threshold. For the purpose of additional anatomical precision, the figures are based on group contrasts overlaid on a surface based representation of the MNI canonical brain using the

SPM surfrend toolbox (written by I. Kahn; http://spmsurfrend.sourceforge.net) and Neurolens (written by R. Hoge; http://www.neurolens.org) for visualisation.

Results

Behavioural Results

On average, participants gave correct responses on 86.8 % of the catch trials (For technical reasons, the accuracy data from one participant were not available for analysis, and the behavioural analysis was conducted on the remaining eleven subjects). As these response trials were cued sparsely, the high level of performance on the catch trials means that we can be confident that participants paid appropriate attention to the stimuli on non-target trials. There were no behavioural differences between the responses for small and large number displays (t(10)= 1.495, p= 0.166).

NeuroImaging Results

A random effects analysis of the neuroimaging data was carried out to evaluate the different areas demonstrating adaptation of the BOLD response to the contrasting paired numerosity trials. To test the general effects of repeating the stimulus and response category, a direct t-contrast was performed on the data averaged across the 3 “within category” repetition conditions, compared to the no-repetition pairs. There was reduced activity most notably in the left superior frontal gyrus, the left middle frontal gyrus and the left superior parietal lobe, including IPS for repeat- vs. different-category trials. The full results are given in Table 8. This demonstrates that adaptation did occur when a response category repeated compared to when paired trials belonged to different categories. Not surprisingly, this overall adaptation effect was not limited to one specific area, and it could reflect repetition of the same pattern, the same number category, the same response or the added requirement for response switching when paired items differed in category.

Table 8. Summary of a random effects analysis contrasting repeated category pairs and different category pairs (X, Y, and Z refer to the stereotaxic MNI coordinates of the centre of activation. The threshold for significance of the clusters reported here was set at a voxel-wise uncorrected p< .001 – whole brain - and a spatial extent of 20 functional voxels).

clustersize	*Z*	*X*	*Y*	*Z*	*Location*
65	4.09*	-26	-54	32	L superior parietal lobe
82	4.69*	-16	4	54	L superior frontal gyrus
52	4.21	-28	12	48	L middle frontal gyrus
22	3.74	-10	34	42	L superior frontal gyrus

* cluster significant at whole brain corrected .05 level

Next, tests were performed to isolate regions that showed more activation for pairs of larger numerosities (including all trial types: identical, number and category repetitions) than for pairs of smaller numerosities. There were significant patterns of activation in bilateral anterior cingulate, bilateral posterior cingulate, bilateral angular gyri and bilateral superior frontal gyri. A whole brain image is provided in Figure 47, with the full table of results given in Table 9.

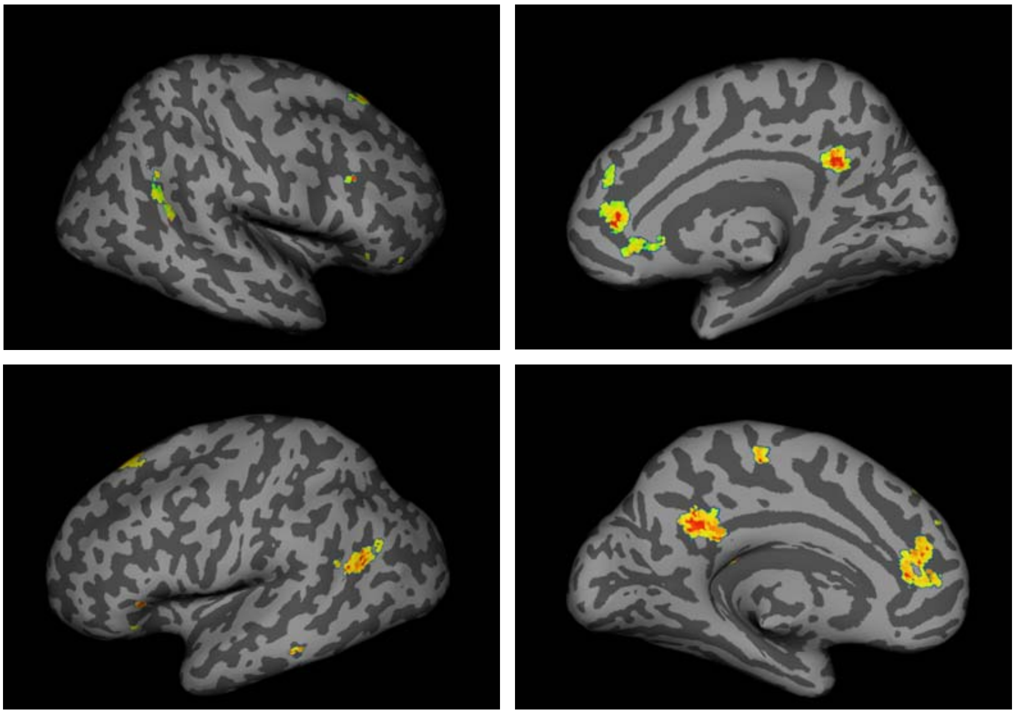


Figure 47. Brain regions that responded more for pairs of large numerosities than for pairs of small numerosities.

Table 9. Summary of a random effects analysis contrasting repeated large number pairs over repeated small number pairs (X, Y, and Z refer to the stereotaxic MNI coordinates of the centre of activation. The threshold for significance of the clusters reported here was set at a voxel-wise uncorrected p< .001 –whole brain - and a spatial extent of 20 functional voxels).

Cluster size	*Z*	*X*	*Y*	*Z*	*Location*
242	4.61*	-44	-62	24	L angular gyrus
122	4.04*	54	-56	20	R angular gyrus
46	4.5	16	32	56	R superior frontal gyrus
59	3.91	-16	32	50	L superior frontal gyrus
29	3.71	46	34	-4	R frontal pole / inferior frontal gyrus
42	4.26	-48	22	0	L inferior frontal gyrus
24	4.53	-6	-28	56	L precentral gyrus
110	5.26*	12	38	4	R anterior cingulate
199	3.92*	-6	40	10	L anterior cingulate
359	4.06*	-8	-50	32	L posterior cingulate
	4.62*	6	-50	32	R posterior cingulate

* cluster significant at whole brain corrected .05 level

To assess whether there was a number-specific adaptation effect, we compared activation when the exact same number was repeated (but in a different pattern) vs. when consecutive trials had different numbers from the same response category. A conjunction contrast was conducted for both response categories (small and large numerosities). Relative to pairs of different numbers from the same response category, there was suppressed activation in early visual areas in the lingual gyrus (Z= 3.94, see Table 10), as well as superior and inferior frontal and precentral gyri. The suppression in the lingual gyrus was bilateral, although it was only a small cluster on the left (MNI -20 -62 -2). It is probable that the posterior activation cluster was even larger, but many early visual areas were missed out in our scanning settings in order to cover all of the parietal and frontal lobes. The adaptation effect in early visual areas is consistent with these regions coding for visual properties that were held constant for same number pairs but not for different number pairs, such as the area of field occupied by patterns. The full table of results is given in Table 10.

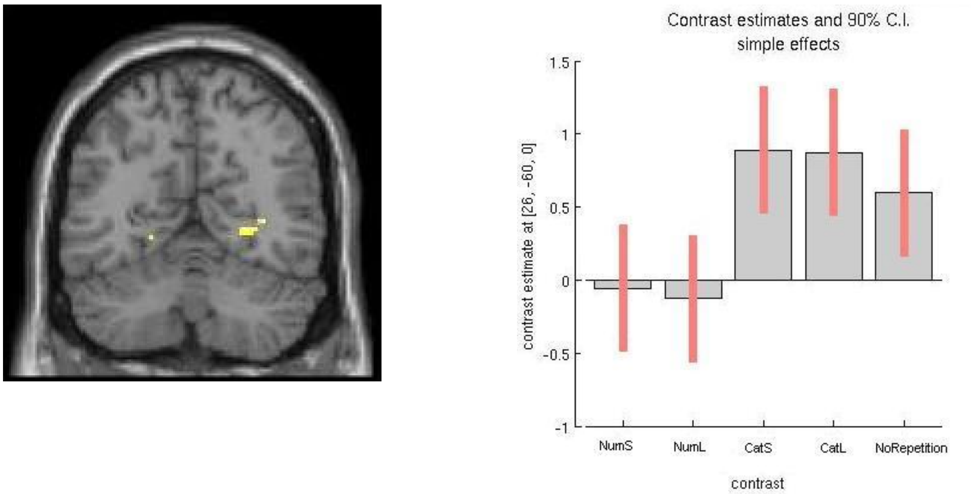
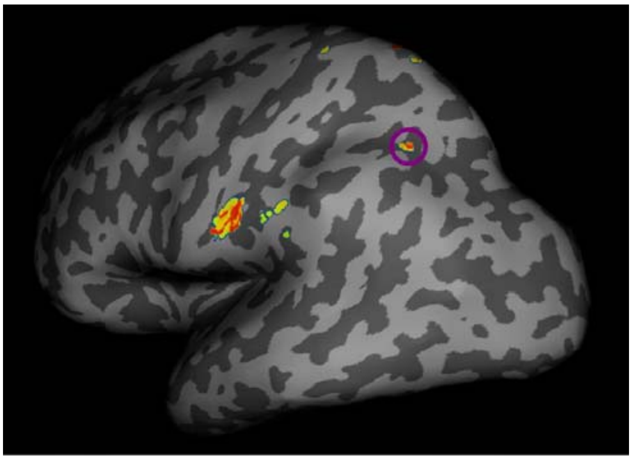


Figure 48. The bilateral lingual gyrus demonstrated reduced activity when the same number of elements was repeated compared to when consecutive trials had different numbers from the same response category. A conjunction contrast is depicted across both small and large categories overlaid on a single-subject representation of the MNI canonical brain.

Table 10. Summary of a random effects analysis of a conjunction contrast of small and large repeated numerosities < repeated response category, different numerosities. (X, Y, and Z refer to the stereotaxic MNI coordinates of the centre of activation. The threshold for significance of the clusters reported here was set at a voxel-wise uncorrected p< .001 –whole brain - and a spatial extent of 20 functional voxels)

clustersize	*Z*	*X*	*Y*	*Z*	*Location*
49	4.06	-10	12	48	L paracingulate gyrus
56	3.94	26	-60	0	R Lingual Gyrus

The main interest of the study, however, is whether there is number-specific adaptation for small numbers in the subitizing range that is not present for the larger numerosities. To assess this, differences in adaptation were assessed between pairs with the same small numerosity compared to pairs with a different small numerosity (but same response category), while exclusively masking this difference for the larger numerosities. This contrast revealed a robust difference in activation in the left IPS, the left superior parietal lobule, the left inferior temporal gyrus, the left postcentral gyrus and the right putamen (Figure 49,Table 11).



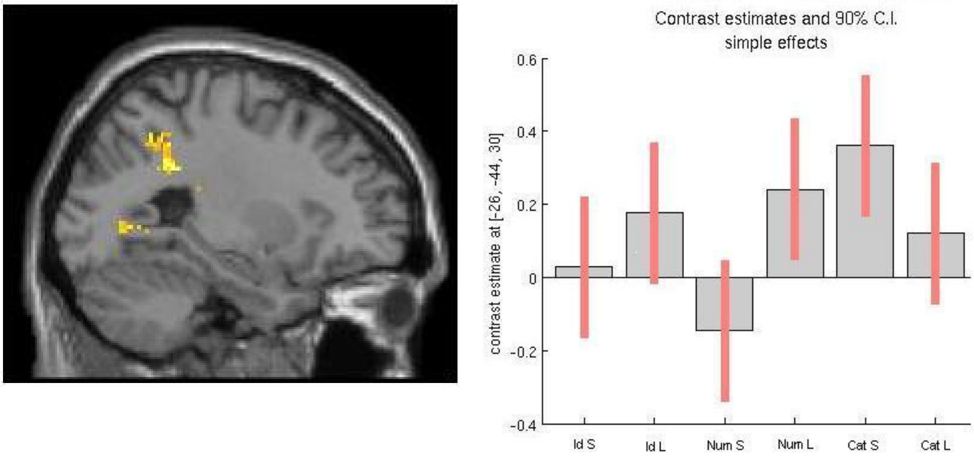


Figure 49. Adaptation specific to small numbers, in the left IPS, when the same number of subitizable elements was repeated compared to when consecutive trials had different numbers from the same (small) response category. This contrast was masked exclusively by the same contrast for larger numbers and is thus specific to small numerosities. For visualisation purposes, the group contrasts were overlaid on a single-subject representation of the MNI canonical brain and the threshold was lowered.

Table 11. Summary of a random effects analysis where activation for small number pairs was less than for small category pairs, masked exclusively by the same contrast for the large number pairs (p<.05 whole brain uncorrected). The threshold for significance of the clusters reported here was set at a voxel-wise uncorrected p< .001 –whole brain - and a spatial extent of 20 functional voxels)

clustersize	*Z*	*X*	*Y*	*Z*	*Location*
40	4.88	-38	-60	0	L inferior temporal gyrus
22	4.65	-26	-44	30	L Intraparietal Sulcus
27	4.51	16	16	48	R superior frontal gyrus
51	4.49	-54	-18	30	L postcentral gyrus
26	3.69	34	-42	-8	R lingual gyrus
26	4.02	-16	-50	70	L superior parietal lobule
51	4.00	26	20	0	R putamen
33	3.52	34	-24	-2	R hippocampus

Discussion

Small number adaptation

These results confirm that repetition of the same small number (presented in a different pattern) elicits more neuronal adaptation in the left intra-parietal sulcus (IPS) and inferior temporal gyrus than repeated presentations of displays with different small numbers. This effect was specific to small numbers. The IPS is traditionally associated with the processing of symbolic numbers (e.g. Dehaene, haene-Lambertz, & Cohen, 1998), and although there are recent reports that bilateral IPS also responds to quantities of dots (e.g. Piazza, Pinel, Le Bihan, & Dehaene, 2007), it has never been shown before to be involved specifically in small exact numerosities more than in larger quantities Recent papers investigating the representation of non-symbolic numerosities in the IPS have found overlapping activations for non-symbolic and symbolic numbers when participants passively viewed sequences of numerosities. However, typically only 2 quantity categories have been used in these studies, and participants were always made aware of the exact quantities presented (Piazza et al., 2007; Cantlon, Brannon, Carter, & Pelphrey, 2006). As noted in the Introduction, it is possible that participants coded these numerosities in a symbolic way during the experiment. Indeed, when Shuman and Kanwisher (2004) used 8 different numerosities in a passive viewing task, no number-specific adaptation was found in the IPS. In their experiment, participants were also not made aware of the exact quantities being presented, and no number-specific task was involved. However, Shuman and Kanwisher (2004) did not make the distinction made here between small subitizable numerosities and larger numbers, and so they did not observe the specific effect for small numbers.

The present data support the argument for there being a distinct subitizing process which gives rise to an exact representation of small numbers (e.g. ‘two’). When this process is repeated a neural adaptation effect is apparent. When consecutive small numbers differ, however, contrasting values are computed and there is minimal adaptation (Figure 49). This proposal also fits with the suggestion made by Feigenson, Dehaene and Spelke (2004), that there are two distinct core systems of numerical representation that are independent of learning or culture. The first system is concerned with approximate representations of large numerical quantities. This core system gives us a noisy representation of number and is sensitive to the ratio between numerosities. It can be thought to underlie the process of estimation. The second core system deals with the precise representation of small numbers. This second system can be thought to underlie the immediate parallel processing of smaller numerosities – subitization. This second "exact" system is sensitive to absolute number, as opposed to the first core system which is sensitive to the inter-relations between numerosities. On a similar note, Castelli et al. (2006) investigated the distinction between perceiving exact vs approximate quantities in terms of a difference between discrete and analogue quantities. They presented participants with hues of blue and green and these were either presented in discrete rectangles separated by gray background (exact quantity), or a smoothing function blurred the boundaries between the different hues (approximate quantities). When deciding whether there was more green or more blue present, the traditional number area (bilateral IPS) was more active when participants were processing discrete (exact) quantities, compared to analogue (approximate) quantities. Similarly, Piazza and colleagues (2006) demonstrated that exact numerosity judgements (when counting) are associated with greater activation of a left-lateralized fronto-parietal network compared to approximate numerosity judgements (when estimating).

Although only discrete quantities were used here (unlike Castelli, Glaser, & Butterworth, 2006; but similar to Piazza, Mechelli, Price, & Butterworth, 2006), the present results could be interpreted as reflecting this discrete quantification process since, when small exact numerosities are repeated, use of the same subitization process will generate a common discrete number representation irrespective of the analogue patterns presented (which changed, when the same exact numbers were repeated). At larger numerosities, though, the similarity of the analogue patterns, even when the exact numbers differ, reduces behavioural differences between the repetition conditions (see Chapter 5).

The region of the intra-parietal sulcus showing adaptation specific to small numbers has also been implicated in visual short-term memory tasks. Xu and Chun (2006; 2009) have recently argued from fMRI data with normal observers that a region around the inferior intra-parietal sulcus responds to the presence of a maximum of about 4 individuated objects (see also Todd & Marois, 2004). This suggests that the adaptation effects here may reflect facilitated coding of the same exact small number if VSTM, rather than re-engagement of the same visual encoding processs.

A contrasting account of the efficient enumeration of small numbers, which does not assume a distinct subitization process, is that participants enumerate small numbers by recognizing their associated, distinct patterns (Logan & Zbrodoff, 2003; Mandler & Shebo, 1982). The adaptation effect in the lingual gyrus (Figure 48) is consistent with repetition of low-level visual properties of the stimuli, but this held across small and large numerosities alike, and so is not specific to a pattern recognition process for small numerosities. If pattern recognition were critical to the neural adaptation effects, then we might expect to see adaptation taking place in brain regions associated with shape processing, such as the lateral occipital complex where shape-based adaptation has been reported (Kourtzi & Kanwisher, 2001). Human imaging studies have implicated a large object-related cortical region referred to as the lateral occipital complex (LOC), which is located primarily ventral and anterior to human MT/V5 and lateral to retinotopic regions V4/V8. Kourtzi and Kanwisher (2000) showed that LOC in ventral occipitotemporal cortex of humans extracts and represents two-dimensional shape. The activation in the inferior temporal gyrus that was implicated in exact small number processing (Table 11) could be linked to this, as this area is one of the higher levels of the ventral stream of visual processing, associated with the representation of complex object features, such as global shape and visual object recognition. Previous studies have implicated the inferior temporal gyrus to be part of the LOC, especially in primates (e.g. Gross, 1992), but also in humans (Grill-Spector et al., 1999). Denys et al. (2004) equally found shape-sensitive regions in humans and primates to include a large portion of the posterior inferior temporal gyrus.

Increased activation for larger numerosities.

In addition to the selective adaptation effects found for repeats of the same small numbers, there were also multiple regions that showed increased activation when large relative to small numbers were presented, including bilateral angular gyri, anterior and posterior cingulate and other regions within pre-frontal cortex (superior and inferior frontal gyri). The angular gyrus has been implicated in studies on calculation and the retrieval of arithmetic facts (e.g. Grabner et al., 2009). The neuropsychological syndrome associated with problems in more general number understanding and mental calculation is dyscalculia, and this has also notably been associated with lesions to the left angular gyrus. Damage to the angular gryus is also linked to Gerstmann’s syndrome, where acquired dyscalculia co-occurs with finger agnosia, left-right disorientation and agraphia (Gerstmann, 1940).

The extra regions found here have been shown previously to be involved in the counting of large over small numbers. Sathian et al (1999) found counting larger numbers to activate bilateral superior parietal lobe/intraparietal sulcus, right inferior frontal regions, and anterior cingulated. Similarly, Piazza and colleagues (2003) found a large network of occipital (calcarine, middle occipital), parietal (anterior and posterior IPS), insular, prefrontal and subcortical areas that were more activated for counting than subitizing. It is likely this reflects various operations coming into play when large quantities are presented – not just processes involved in estimation but possibly some residual counting processes and greater demands on working memory. Although the basic task only required the estimation of displays, it cannot be ruled out that participants also counted the items on some occasions.

Conclusion

This study assessed the coding of non-symbolic numerosities in an indirect way, using an approximate estimation task that did not require participants to distinguish between the actual numerosities presented. Despite this, there was evidence for a neural difference between larger and smaller numerosities specific to when the exact same quantity was repeated (for small numbers, relative to a different-quantity, same response baseline). This suggests that participants classified exact numbers within the small numerosity using a subitization process that recruits the IPS and the inferior temporal gyrus. We link this to a specific visual process of subitization.

CHAPTER 7:

GENERAL DISCUSSION

Overview of the findings

The work presented in this thesis has explored attentional mechanisms and number representations in visual enumeration and estimation through a variety of methods. I have first distinguished between the different attentional modes underlying estimation and enumeration in an in-depth single case study of a patient with simultagnosia. I then demonstrated that, in visual enumeration, subitizing and counting are dissociable processes and they rely on different necessary brain structures. This was done through a neuropsychological single case study as well as through the first large sample neuropsychological group study using a voxel-by-voxel correlation method. Subitizing was then related back to estimation, through a series of behavioural reaction time experiments, where participants adopted a distributed attentional mode through an estimating task. Under these estimation conditions, the findings suggest that subitizing is an automatic process, and that it leads to exact small number perception, which contrasts with an approximate number perception for the larger numerosities when estimating. Finally, a functional MRI study was conducted to highlight the brain regions that are activated for subitizable numerosities, but not for larger numerosities in such an estimation task under distributed attention conditions. This provided converging evidence for subitizing being a specialized and automatic process and leading to an exact number representation.

In the first empirical chapter, the attentional mechanisms behind enumeration and estimation were explored, in a single case study of a Balint’s syndrome patient, GK. Due to his simultanagnosia, GK has a severe impairment in visual enumeration (though his counting of non-visual items was intact). It was hypothesised that estimation and counting rely on different attentional processes, with Focused attention, using a narrow attentional window, being adopted for counting; and a more Distributed attention mode, covering a wider spatial area, being adopted for estimating.

The results showed that GK was very poor at counting, with his errors on counting being at best only loosely related to the numbers of items present. On the other hand, GK was above chance at estimating the numbers of items present (Exp. 2.1). In addition, his counting performance was not helped when the display durations were limited to the exposures used for estimating (Exp 2.2) and when given the same task (decide which of two displays contains more items), his performance is much better when asked to estimate (using a distributed attentional mode) compared to when he is forced into a focussed attentional mode (by asking him to count the items in order to make the 2AFC decision) (Exp 2.3). These last two results further indicate that, when in a focused attention mode, GK cannot explicitly use the information potentially available when a distributed mode of attention is employed.

The results when estimating, indicate that patients with Balint's syndrome cannot be characterized as simply having an abnormally narrowed spatial window of attention (cf. Thaiss & Debleser, 1992). The data also indicate that such patients are able to attend to more than one element in a display, when a distributed mode of attention is adopted. This last conclusion is also supported by evidence for implicit processing of 'the whole'. For example, even though patients report seeing only one thing at a time, conjunction errors occur when there are multiple items present, suggesting that multiple features at least are still processed (Friedmanhill et al., 1995; Humphreys et al., 2000). Similarly, simultanagnosics can attend to multiple features within objects but show deficits when asked to attend to the spatial relations between separate objects (Cooper & Humphreys, 2000; Shalev & Humphreys, 2002) and in hierarchical stimuli (such as those used by Navon, 1977), RTs to local elements can be speeded when the global forms are consistent rather than inconsistent with the local letter identities (Karnath et al., 2000, Shalev et al. 2005), despite patients typically being biased towards the local elements in such displays.

However, when counting and in a focussed attention mode, it is indeed likely that GK operated through an abnormally narrowed attentional window, a finding that is supported by the findings of Experiment 2.6, where the vision of normal participants was artificially limited and a similarly impaired performance on enumeration of visual items was found.

I further explored how grouping of the elements (by proximity, colour and collinearity) impacted on GKs performance in the two tasks (enumerating and estimating). The results showed that magnitude estimation but not counting was facilitated by using elements that grouped more easily and by presenting the elements in regular configurations. In contrast, counting was facilitated by placing the elements in different colours whilst magnitude estimation was disrupted (Exp 2.1). This demonstrates that when in a focused attention mode GKs performance is limited due to an impaired explicit representation of visual space. Indeed, counting individual colour types is possible even with poor location codes, so that colour counting is advantaged (Exp 2.5). This, in addition to GK's intact ability to count when stimuli are presented in modalities other than vision (e.g., the elevator counting task in the Test of Everyday Attention (Robertson et al., 1991), indicates that there is no impairment of the exact number system per se (Feigenson et al., 2004) or a more general number problem, such as dyscalculia (Berger, 1926); rather there is a deficit specifically in the visual coding of number. Colour types may be detected by activation in separate colour maps, within a 'colour space', that GK remains sensitive to, though he has difficulty recovering the location of any activity within each map. This is consistent with the argument that subitizing and counting are inherently spatial processes, operating on a map of stimulus locations (Watson & Maylor, 2006). It thus appears that the posterior parietal cortex is critical for the explicit recovery of such location codes, for separate objects (see also Humphreys, 1998; Xu & Chun, 2009; Riddoch et al., in press).

In a follow-up study, the extent of GK's perception in a distributed attentional mode was further explored, by assessing whether he has a representation of the visual statistics of displays. Overall, this study demonstrated that automatic statistical processing of colour and size is indeed possible in simultanagnosia, when operating through a distributed mode of attention (see Appendix 2).

The third and fourth chapters both were neuropsychological investigations into whether subitizing and counting truly are separate processes and can be dissociated following brain damage. In Chapter 3, an in-depth case study was presented on a patient, MH, who showed a marked dissociation in the visual enumeration of small compared to large numerosities. MH presented with a preserved ability to subitize (both in demonstrating a perfect accuracy as well as a very shallow RT slope) along with a marked inability to accurately count numerosities that fall outside the subitizing range (Exp 3.1). His non-visual counting was intact and he was able to do simple sums as well, demonstrating that his inability to count items in a visual display cannot be explained by a general number comprehension problem. When larger numbers of items were spatially grouped into 2 subitizable units, performance dramatically improved (Exp 3.2). It seems that here, spared subitization processes can be used to support impaired counting. However, when the displays were grouped into subitizable subgroups on the basis of colour (e.g. 3 red and 2 green dots), this did not aid MH's performance (Exp 3.3a), despite his being sensitive to colour segmentation. It thus appears that spatial grouping still dominates, and overrides any colour effects (Exp 3.3b). Again, this is consistent with the subitizing and counting being inherently spatial processes (Watson & Maylor, 2006). In addition, MH's counting improved when a motor record of counting could be maintained (Exp 3.4), suggesting that tapping functioned as a visuo-motor aid, helping MH remember the locations he already visited. It appears that the visuo-motor response can provide a substitute spatial representation, when visuo-spatial memory is impaired (see also Forti & Humphreys, 2004). The data presented in this chapter can thus parsimoniously be accounted for in terms of impaired visuo-spatial memory. The findings support the argument that at least some processes are specific to counting and are not required for subitization – in particular spatial coding and memory for previously inspected locations.

In the fourth chapter, a large neuropsychological group study was presented, assessing visual enumeration in 34 patients with brain damage. Patients were not selected on their lesion locations or their performance. Instead, we measured subitizing and counting of random dot patterns for all patients and we used an observer independent voxel-based correlational method to associate damaged brain tissue with impaired enumeration behaviour. In accordance with behavioural and fMRI data, it seems that subitizing and counting can be separated on a neuro-anatomical basis. Here, the necessary regions associated with different levels of impairment in subitizing and counting were demonstrated. Counting impairments were found to be associated with damage to a large fronto-parietal network, including the left angular gyrus, and higher visual areas. This matches fMRI activations in counting tasks (Sathian et al., 1999; Piazza et al., 2003). The angular gyrus damage may disrupt the ability to assimilate exact number, critical not only to counting but also to general numerical cognition. Damage to the angular gyrus has been linked to Gerstmann's syndrome and dyscalculia (Gerstmann, 1940; Mayer et al., 1999; Rusconi et al., 2009). The damage to more frontal regions, associated with poor counting, may be related to working memory and visuospatial attention as well as saccadic behaviour (e.g. Postle et al., 2000).

In contrast, poor subitization was linked to damage to occipital areas, both early (around the calcarine sulcus) and higher visual areas (around the lateral occipital sulcus) and precuneus. The evidence for changes to visual processing regions and the precuneus in relation to impaired subitization fits with the proposal that subitization depends on the efficient, parallel apprehension of a small number of objects. The early visual areas were also found to be associated with subitizing in fMRI studies on visual enumeration (Sathian et al., 1999; Piazza et al., 2002; 2003). The lateral occipital sulcus is part of the functional Lateral Occipital Complex, which has been found to underly shape and 2D object processing (e.g. Grill-Spector et al., 1999; Kourtzi & Kanwisher, 2000) and could be linked to pattern matching accounts of subitizing, where it is deemed that object recognition of familiar patterns (e.g. a triangle for 3 dots) underlies the fast subitizing performances (e.g. Mandler & Shebo, 1982; Logan & Zbrodoff, 2003). The precuneus, found to be associated with poor subitizing performance has been suggested to be crucial in the perception of the 'whole' (Himmelbach et al., 2009). Severely impaired subitizing performance was also related to the clinical disorder of simultanagnosia, which is linked to a poor representation of the 'whole' (e.g. Coslett & Saffran, 1991; Friedmanhill et al., 1995). Apart from these grey matter regions, poor subitization was also associated with reduced WM in part of the corona radiata in the vicinity of the parieto-occipital sulcus. This fits with proposals suggesting that simultanagnosia is linked to slowing of information processing speed when measured within the framework of the theory of visual attention (Bundesen, 1990), but not impaired VSTM itself (e.g. Duncan et al., 2003). This slowing of visual processing speed could link to the white matter disconnection, while damage to the inferior IPS itself is not selectively associated with poor subitization.

Chapter 5 related the findings on subitizing small numbers back to the different attentional modes. Here, I assessed whether different processes underly the estimation of small (subitizable) numerosities compared to larger numerosities (that would normally require counting). This was done through a series of behavioural reaction time experiments where participants adopted a distributed attention mode in an estimating task. Performance was contrasted when consecutive displays were identical, maintained their pattern but shifted position, had the same number but changed patterns, and had different numbers but were assigned to the same response category. The results from the different experiments in this chapter all showed that for displays with up to 5 items there was a clear drop in performance when items repeated from the same response category relative to when displays repeated with the same number. This result was much less evident with larger display sizes, where typically, there was no difference in RTs when the same or a different large numerosity was repeated. The difference only emerged when the items within the large display sizes were made highly discriminable, and even then it remained a much smaller effect (Experiment 5.4).

Using random displays and only identical, number and category repetitions (in Exp 5.1a), the basic pattern of performance was first established. The advantage for same number over same category trials, for the small display sizes, could have been due to the same number displays having greater visual similarity than the same category displays (Logan & Zbrodoff, 2003). Alternatively, this advantage may have been due to the same exact value being computed in the same number condition, whereas different number values are computed across trials in the category repeat condition. Sensitivity to exact number may reflect the operation of a subitization process based on parallel assimilation of the elements (Trick & Pylyshyn, 1989), rather than pattern recognition.

Further experiments were then performed to explore the pattern matching hypothesis. Experiment 5.1b was designed to enable pattern recognition to play a stronger role. Here the displays contained familiar patterns for all numerosities, enabling pattern recognition processes to come into play for both small and large display sizes. Again, the same number advantage was greater for small relative to large display sizes. The benefit of repeating the identical pattern tended however to be greater for larger compared to smaller numerosities. The basic pattern of contrasting results with small and large display sizes (greater advantage for same number repetitions for small than large numerosities) was found even though the subsequent experiments controlled for display area, inter-item spacing and average luminance (Exp 5.2 - 5.4).

In order to further tease apart contributions from visual similarities, pattern recognition and automatic abstract small number assimilation, I introduced heterogeneous dot displays, where visual similarity was manipulated by varying or not varying the proportions of the polarities that constitute the numerosity display. New types of repetition condition were also introduced, where consecutive displays (i) maintained their pattern but shifted position, (ii) had the same proportions and the same number but changed patterns, (iii) had different proportions and the same number but changed pattern and (iv) had a different number (and pattern) but were assigned to the same response category. These different types of repetitions were first rated on pattern similarity in pairs (Exp 5.3a) and were subsequently used in the same type of behavioural serial repetition experiments as before (Exp 5.3b and 5.3c). For these displays, patterns were judged more similar if the relative balance of white to black items was maintained than if this changed. However, the effect of repeating the same exact number was the same irrespective of whether the proportions of black to white stimuli changed; whereas with larger numerosities, carry-over effects were stronger if the proportion of black to white elements was maintained. This suggests that pattern similarity might have been more important for larger than for smaller numerosities. In addition for the small subitizable numerosities there was no added benefit from keeping the pattern and shifting its location compared with presenting a completely different pattern (in the number repeat condition). For larger numerosities, there was some added benefit from repeating the same pattern, suggesting some sensitivity to the overall pattern in this case. From these experiments, the data suggest that visual similarity, alone, cannot explain performance in the numerosity judgement task. The data are consistent with an automatic subitizing process leading to small numbers being represented in terms of exact number. The rapid assimilation of small exact numbers appears to involve two processes: the recognition of familiar patterns and the parallel assimilation of the stimuli (subitization). These processes are distinct from magnitude estimation, which occurs with larger displays, and generates approximate rather than exact number representations.

The final empirical chapter (Chapter 6) assessed the relations between coding small and larger numerosities under distributed attention using fMRI. This study assessed the coding of non-symbolic numerosities in an indirect way, using the approximate estimation from Chapter 5, which did not require participants to distinguish between the actual numerosities presented. There was evidence for a difference in processing larger and smaller numerosities specific to when the exact same quantity was repeated (for small numbers, relative to a different-quantity, same response baseline). The data support the argument for there being a distinct subitizing process which gives rise to an exact representation of small numbers (e.g. ‘two’). When this process is repeated a neural adaptation effect is apparent. When consecutive small numbers differ, however, contrasting values are computed and there is minimal adaptation

Repetition of the same small number (presented in a different pattern) elicited more neuronal adaptation in the left intra-parietal sulcus (IPS) and inferior temporal gyrus than repeated presentations of displays with different small numbers. This effect was specific to small numbers. This suggests that participants classified exact numbers within the small numerosity using a subitization process that recruits the inferior temporal gyrus and the IPS. The IPS is traditionally associated with the processing of symbolic numbers (e.g. Dehaene et al., 1998) and has been shown to be more active for discrete, exact quantities than approximate quantities (Castelli et al., 2006; Piazza et al., 2006). The results from this fMRI study can be interpreted as reflecting a discrete quantification process where use of the same subitization process will generate a common discrete (and symbolic) number representation irrespective of the analogue patterns presented (which changed, when the same exact numbers were repeated). At larger numerosities, though, the similarity of the analogue patterns, even when the exact numbers differ, reduces behavioural differences between the repetition conditions (see Chapter 5), and are therefore likely not to be coded in discrete symbolic terms. The region of the intra-parietal sulcus showing adaptation specific to small numbers has also been implicated in visual short-term memory tasks, with the IPS responding to a maximum of 4 objects – the capacity limit for VSTM and the upper limit for subitizing (Todd & Marois, 2004; Xu & Chun, 2006; Xu & Chun, 2009). Hence the adaptation effects here could be due to representation of the same ‘load’ of items in VSTM. The activation in the inferior temporal gyrus that was implicated in exact small number processing could be linked to pattern and object recognition (hypothesised to be underlying efficient subitization – e.g. Mandler & Shebo, 1982), as this area is one of the higher levels of the ventral stream of visual processing, associated with the representation of complex object features, such as global shape and visual object recognition (e.g. Grill-Spector et al., 1999; Denys et al., 2004).

In addition to the selective adaptation effects found for repeats of the same small numbers, there were also multiple regions that showed increased activation when large relative to small numbers were presented, including bilateral angular gyri, anterior and posterior cingulate and other regions within pre-frontal cortex (superior and inferior frontal gyri). This matches fMRI results, where the angular gyrus is associated with calculation (e.g. Grabner et al., 2009) and neuropsychological data implicating the angular gyrus in Gerstmann’s syndrome (Gerstmann, 1940) and dyscalculia (Kadosh & Walsh, 2007). The extra regions have previously been shown to be involved in the counting of large over small numbers (Sathian et al., 1999; Piazza et al., 2003). It is likely this reflects various operations coming into play when large quantities are presented – not just processes involved in estimation but possibly some residual counting processes and greater demands on working memory.

Subitizing and counting: dissociable processes

Counting

Counting can be dissociated from subitizing. In this thesis I have provided novel evidence from two separate studies towards supporting this idea. In the first study, Chapter 3, an in-depth report of a patient with posterior parietal lesions, MH, demonstrated that it is possible to have a preserved ability to subitize (both in accuracy and RTslope), yet a marked inability to count more than 4 elements. This inability to count was not due to more general number comprehension problems or acalculia, as MH could enumerate auditory stimuli and could do simple sums. In addition, there were differential effects of particular variables on the two parts of the enumeration function: Subitization was not affected by grouping or by segmenting the stimuli into colour groups, whereas counting was helped by splitting the items into subitizable-subgroups (spatial grouping). Counting was also aided by making MH tap items that he counted, whereas subitization slopes tended to increase. I suggest that a severe visuo-spatial memory deficit can account for these results demonstrating that there is a particular visual process subserving subitization that is spared here, along with an impaired counting function. The data do not differentiate, however, whether subitization is spared due to MH maintaining a preserved number of FINSTs (Trick & Pylyshyn, 1989; 1993) or due to him using a pattern recognition process (Mandler & Shebo, 1982).

The second study to demonstrate that a specific process underlies counting is the large sample VBM study presented in Chapter 4. Thirty-four patients were assessed on their visual enumeration performance in a standardized manner and assigned to different groups based on their relative level of impairment (compared to controls and compared to other patients) in subitizing and counting. By doing this, damaged brain regions that corresponded to poor counting performance could be separated out, while covarying out the subitizing impairment levels. The results showed that there were indeed regions associated with increasing impairments in counting, irrespective of subitizing.

The above findings (from both studies) support the idea that even though subitizing may not be ‘pre-attentive’ (e.g. Vetter, Butterworth, & Bahrami, 2008; Olivers & Watson, 2008), it does not require the same processes as counting does. At least some processes are specific to counting and are not required for subitization – in particular spatial coding and memory for previously inspected locations.

Subitizing

Can subitizing also be selectively impaired, with a preserved counting ability? Previous studies have shown that subitizing can be selectively impaired, when judged in terms of subitizing speeds (e.g. Lemer et al., 2003; Ashkenazi et al., 2008; Halpern et al., 2007). These patients tend to adopt a serial counting strategy even for the smaller numerosities. Subitizing may be mediated by a heuristic process (which may be based on visual pattern recognition, or a parallel assimilation process specific to small numbers). However, when this heuristic process is damaged, then the patient has to rely on the the more effortful process of counting.

When the enumeration of small numbers is severely impaired (based on accuracy rather than RTs), counting will also be impaired. If, even when using a serial strategy, a patient is unable to enumerate small numbers, counting larger numbers will automatically be impaired as well. This was found here in the large study examining enumeration and estimation in a simultanagnosic patient (GK).

The VBM study reported in this thesis (Chapter 4), took into account both accuracy and reaction time slopes in order to construct an efficiency slope measure, which the levels of impairment were based on. By doing this, a more graded measure of impairments was introduced (previously patients with severe and mild impairments have been considered separately). Patients were assigned to different groups based on their relative level of impairment. Importantly, the groups reflected differences in the relative severity of impairments compared to the other patients in the sample, separately for subitizing and counting. The results showed that there were separate damaged brain regions that corresponded to poor subitizing performance, while covarying out the counting impairment levels. This suggests that separate areas are crucial for subitizing, this is likely to reflect specific processes underlying subitizing.

Different attentional requirements

GK demonstrated a severe impairment in visual enumeration, but was above chance in estimation tasks. This fits with him operating in a focussed attention mode for counting and a more distributed attention mode for estimating. In addition, GK was more sensitive to grouping between the items when he employed a distributed mode of attention (when estimating rather than counting). Thus in the estimation task only, performance was improved with square patterns, when the elements could group by collinearity when in canonical patterns. This result is consistent with grouping by collinearity being modulated by attention (see also Freeman et al., 2003); grouping by collinearity is stronger when the elements fall in an attended spatial region. This is not to say that the same degree of grouping does not operate without attention (indeed GK's worse counting of items in configurations relative to randomly located stimuli, suggests some degree of pre-attentive grouping; see Gilchrist et al., 1996 for prior evidence), but it appears that grouping interactions are stronger when the elements are attended. This fits with an interactive view of visual processing in which top-down attentional activation combines with bottom-up activity from stimuli to facilitate visual processing (Cinel & Humphreys, 2006; Hochstein & Ahissar, 2002).

The relatively intact estimating performance suggests that GK can adopt a distributed mode of attention, and under this circumstance, process information in parallel (adding to aforementioned evidence on conjunction errors, multiple features and hierarchical stimuli). However, it has been suggested that simultanagnosics are typically poor at maintaining this mode of attention (Shalev et al., 2005), and most often fall back to a default of focused attention, with limited visual processing as a result.

Though his counting of spatially defined items was very poor, his performance improved greatly when asked to count colourtypes. This again fits with GK having a severely impaired explicit representation of the spatial locations of separate objects, resulting in severe difficulties in keeping track of visited locations, causing him to re-count items (at least in a focused attention mode).

Although subitizing is also thought to rely on distributed attention (as is estimating), GK made errors in enumerating displays of even 1 or 2 dots. Interestingly, GK's ability to operate through a distributed attentional mode was not sufficient for a preserved subitizing performance. It seems that subitization may, in addition, require accurate coding of object locations, so that objects can be individuated (cf. Trick & Pylyshyn, 1993; 1994). Xu and Chun (2009) also recently suggested that simultanagnosia reflects an impairment in this individuation process. Without individuation through accurate location coding, subitization is disrupted, despite GK being able to adopt a distributed as well as a focused mode of attention This is in line with recent evidence by Revkin et al. (2008), refuting the view that subitizing may reflect the use of a numerical estimation procedure shared for small and large numbers (Gallistel & Gelman, 1991; Dehaene & Changeux, 1993).

Neural substrate of small and large numerosities

In this thesis, through a multitude of methods (single case neuropsychological studies, VBM analysis of damaged brain tissue as well as fMRI of healthy participants), a picture of the neural regions underlying small and large numerosity representation has emerged.

Small numerosities

Whether it be in visual enumeration or estimation, I have argued that smaller numerosities are automatically subitized and give rise to an exact number representation. Early occipital regions were identified to be necessary for subitization, and in were particularly highlighted through being associated with damaged grey matter in the severely impaired patients in our VBM study (see Chapter 4). These occipital areas could be linked to early visual regions processing location coding and individuation and this may then form the input to regions linked to Visual Short Term Memory (VSTM). This is in line with Xu and Chun (2009)'s neural object file theory which suggests that there is a first stage of forming proto-objects (influenced by grouping), followed by a stage of individuating a small number of objects (fixed capacity limit of 4), and finally these are coded into objects in VSTM. Xu and Chun (2009) found that the inferior IPS represents a small number of objects which are already parsed into 'proto-objects'. This fits with my results, especially given that the IPS was found to be selectively active for small numerosities in the fMRI study (Chapter 6). Xu and Chun (2009) also proposed that simultanagnosia may reflect an impairment in this individuation process, this also fits with the findings from Chapter 2, where a patient with simultanagonosia could not accurately enumerate even a small number of objects. Another possible account is that the IPS is also classically found to be involved in symbolic number tasks (e.g. Dehaene et al., 1998), with the Left IPS specifically representing exact and discrete symbolic number (Castelli et al., 2006; Piazza et al., 2006). In this view, the activation in Left IPS reflects the coding of the small numerosities into exact symbolic terms, in contrast to the larger numerosities, where estimation may only be giving rise to an approximate number representation.

In the VBM study, apart from more early visual regions, damage to the Lateral Occipital Sulcus (LOS) was also found to be associated with impaired subitizing. The LOS is part of the Lateral Occipital Complex (LOC), a functional region found to be responsible for shape processing (e.g. Grill-Spector et al., 1999; Kourtzi & Kanwisher, 2000) and could be linked to pattern matching accounts of subitizing, where it is deemed that object recognition of familiar patterns (e.g. a triangle for 3 dots) underlies the fast subitizing performances (e.g. Mandler & Shebo, 1982; Logan & Zbrodoff, 2003). In the fMRI study, the inferior temporal (IT) gyrus was found to be selectively activated for small numerosities in the estimation task. Although perhaps not traditionally part of the LOC, previous studies have included the inferior temporal gyrus to be part of a great LOC cluster (Grill-Spector et al., 1999; Denys et al., 2004). The IT gyrus is considered to be one of the higher levels of the ventral stream of visual processing, associated with the representation of complex object features, such as global shape and visual object recognition.

Ths brings us to the precuneus, found here to be associated with poor subitizing performance in the VBM study. The precuneus has been suggested to be crucial in the perception of the ‘whole’ (Himmelbach et al., 2009). Severely impaired subitizing performance was also related to the clinical disorder of simultanagnosia, which is linked to a poor representation of the ‘whole’ (e.g. Coslett & Saffran, 1991; Friedmanhill et al., 1995).

Finally, apart from these grey matter regions, poor subitization was also associated with reduced WM in part of the corona radiata in the vicinity of the parieto-occipital sulcus. This lends support to the idea that it is the link between location coding, individuation (early occipital) and VSTM (in inferior parietal regions) that is crucial for subitizing ability.

Large numerosities

In Chapter 3, I presented a single case, MH, who demonstrated a marked inability to accurately count numerosities over 4, along with a perfect subitizing ability of small numbers (both in accuracy and RTs). MH had cortical lesions in bilateral posterior parietal regions, but more pronounced on the left side (including the occipital-parietal borders, intraparietal sulcus and superior parietal lobe). These regions were also found to be necessary regions for visual enumeration of larger numerosities (over 4) in the large sample neuropsychological VBM study, in addition to more frontal regions and the Left angular gyrus. The fMRI study assessed visual estimation, rather than enumeration, but given the jittered paired events design, it is possible that not just processes involved in estimation but possibly some residual counting processes and greater demands on working memory were reflected in the results. Here, the bilateral angular gyri, anterior and posterior cingulate and other regions within pre-frontal cortex (superior and inferior frontal gyri) showed increased activation when pairs of large relative to pairs of small numbers were presented.

I have argued that counting depends on a form of focused attention, in which each item is selected in turn (see Chapter 2). To be successful, such a serial attentional process would need to be supported by other processes, such as spatial indexing, switching attention from item to item and inhibition of return (Laeng et al., 1999; Klein, 2000; Tuholski et al., 2001). In addition Watson and colleagues (Watson et al., 2007) demonstrated a sharp increase in saccades for enumeration of more than 4 items. The frontoparietal network found here to be associated with enumeration of larger numerosities, may be related to these processes, such as working memory and visuospatial attention as well as saccadic behaviour (e.g. Postle et al., 2000). This could also be reflected in the frontal-parietal white matter disconnection found in the VBM study.

A striking commonality between the neuropsychological VBM study and the fMRI study is the prominent featuring of the angular gyrus (bilateral in the fMRI study, and the left angular gyrus in the VBM study) in the representation of larger numerosities. In Dehaene et al.'s triple-code model, the angular gyrus is thought to underlie the 'verbal store', which is used to comprehend and produce spoken and written number names and is also a store of arithmetical facts and tables (Dehaene et al., 2003). fMRI results from more abstract number processing also associate the angular gyrus with calculation and the retrieval of arithmetic facts (e.g. Grabner et al., 2009). In addition, dyscalculia, the neuropsychological syndrome associated with problems in more general number understanding, has notably been associated with lesions to the left angular gyrus. Damage to the angular gryus is also linked to

Gerstmann’s syndrome, where acquired dyscalculia co-occurs with finger agnosia, left-right disorientation and agraphia (Gerstmann, 1940). The findings here suggest that damage to the left angular gyrus predicts difficulties specifically in counting, but not with subitizing. The angular gyrus damage may disrupt the ability assimilate exact larger numbers, critical not only to counting but also to general numerical cognition

Directions for future research

Sensitivity to stimulus properties

There is evidence that subitization depends on the assimilation of particular properties of stimuli – e.g., we are severely limited at counting the numbers of colours in a display (Watson et al., 2005). This suggests that the visual apprehension of small number is contingent on the rapid assimilation of location information (see also Watson & Maylor, 2006). On the other hand, the FINST account of subitization holds that location markers are used also to track moving objects across space (Pylyshyn & Storm, 1988; Trick & Pylyshyn, 1989). A possible future experiment could contrast a location-specific with a FINST account by using the serial response repetition framework (Chapter 5) to compare priming effects when items translate across a display compared (changing locations) with when they change shapes (e.g. expand or contract) but maintain constant locations within a trial. In the ‘number’ priming condition, consecutive trials would then have the same number of stimuli but with different movement patterns (translate up vs down; expand vs. contract). Positive priming from repeating the same exact magnitude of items irrespective of the movement type would support the FINST account, whereas priming confined to when items have constant locations within a trial would support a more location-based apprehension process (due to specific recruitment of the same locations).

Future research could also try to further tease apart the contribution of pattern recognition to efficient subitization. The work presented here has suggested that effects of small number repetitions cannot solely be attributed to pattern recognition. However, similarity and pattern/object recognition do seem to play a role and this idea was strengthened by findings suggesting LOC is involved specifically in subitizing and small number representation. A serial reaction time experiment comparing repetition effects for small magnitudes, when the constituting items are all the same colour or different colours (see also Watson & Maylor, 2006 for prior work on visual enumeration) may further manipulate pattern similarity. Is there exact number priming, for small magnitudes, from a same colour to a different colour trial, and is the effect size the same as when items have the same colours (repeat same- or repeat different colour displays) across trials?

Pattern priming will be affected by whether the colour relations are maintained or differ across trials, since grouping between the elements will change as the number of items within each colour group varies. If small numbers are apprehended using a process separate from pattern recognition, and this process operates independently and in parallel across the items, then this parallel apprehension process should be unaffected by grouping, thus predicting that exact number priming will be equally large across the same and different colour-group conditions (measured against the category priming baseline). In other words, if exact priming of small magnitudes is independent of pattern recognition, then the effect should be immune to effects of changing colours. On the other hand, any advantage for repeated ‘patterns’ over repeated ‘numbers’ should be stronger with repeated colours. A further experiment could then establish the generality of this by varying grouping by shape rather than colour within the displays (e.g., using squares and circles of a single colour).

Effects of attention

Future research could also entail further tests on the interplay between attention and visual apprehension. For example, an experiment where participants carry out a magnitude judgement task to arabic numerals (e.g. <5 ?) appearing in random locations in their left and right fields. Simultaneous with the numeral a small number of elements can be presented in the background. If subitizing is indeed automatic; then RTs to the numerals should be faster on trials where the simultaneously presented elements have a congruent magnitude relative to when they have an incongruent magnitude (a form of Stroop effect). If this holds, then a series of experiments can be set up to examine how this effect varies as a function of the number and the pattern of the irrelevant elements. Based on the data reported in this thesis; it can be hypothesised that interference from the elements on magnitude judgements to numerals will increase when displays have the same exact number of elements relative to when they have different numbers (the exact number priming effect).

With this paradigm, a manipulation of attention could be done by visual pre-cueing – with correct location cues for the Arabic numerals leading to focussed attention; whereas under divided attention conditions cues may appear at all possible locations for the numeral). We will then examine if this effect is reduced under conditions of focused attention, consistent with visual apprehension being contingent on participants maintaining a distributed attentional state. Note that this is one reason why simultanagnosic patients may be impaired at assimilating even small visual magnitudes.

A similar set-up could be used to test effects of spatial attention with patients with chronic biases in spatial attention. Here, we could assess whether there is still an exact small number priming effect when elements fall in the patients' impaired field, and whether this varies in magnitude from effects when the elements fall in the spared field. Effects from elements in the impaired field would indicate apprehension operating without full attention (similar to findings by Vuilleumier & Rafal, 1999), while evidence for increased effects from elements in the intact field would indicate that apprehension is nevertheless modulated by attention.

A final different avenue would be to explore whether a similar paradigm to the one I have used to dissociate between different attentional processes in neuropsychological cases could be employed to examine visual processing abilities in autistic individuals. Individuals with Autism Spectrum Disorder (ASD) often have a tendency to focus on details of an object rather than viewing objects as entities. Frith (1989) proposed that this is a result of “Weak Central Coherence”, with some individuals with ASD struggling to use all elements of a stimulus to derive full meaning. If there is a local processing bias in ASD, it would be interesting to assess whether this would override the efficient subitizing process (assumed to be based on distributed attention), and whether manipulations of grouping (e.g. canonical patterns) would influence the enumeration function in comparison to IQ matched controls.

REFERENCES

Acres, K., Taylor, K. I., Moss, H. E., Stamatakis, E. A., & Tyler, L. K. (2009). Complementary hemispheric asymmetries in object naming and recognition: A voxel-based correlational study. *Neuropsychologia, 47,* 1836-1843.

Andersson, J. L. R., Ashburner, J., & Friston, K. (2001). A global estimator unbiased by local changes. *Neuroimage, 13,* 1193-1206.

Ansari, D., Dhital, B., & Siong, S. C. (2006). Parametric effects of numerical distance on the intraparietal sulcus during passive viewing of rapid numerosity changes. *Brain Research, 1067,* 181-188.

Ansari, D., Lyons, I. M., van Eitneren, L., & Xu, F. (2007). Linking visual attention and number processing in the brain: The role of the temporo-parietal junction in small and large symbolic and nonsymbolic number comparison. *Journal of Cognitive Neuroscience, 19,* 1845-1853.

Antell, S. E. & Keating, D. P. (1983). Perception of Numerical Invariance in Neonates. *Child Development, 54,* 695-701.

Ariely, D. (2001). Seeing sets: Representation by statistical properties. *Psychological Science, 12,* 157-162.

Ashburner, J. & Friston, K. J. (2005). Unified segmentation. *Neuroimage, 26,* 839-851.

Ashkenazi, S., Henik, A., Ifergane, G., & Shelef, I. (2008). Basic numerical processing in left intraparietal sulcus (IPS) acalculia. *Cortex, 44,* 439-448.

Atkinson, J., Campbell, F. W., & Francis, M. R. (1976). Magic Number 4 +/- 0 - New Look at Visual Numerosity Judgements. *Perception, 5,* 327-334.

Balakrishnan, J. D. & Ashby, F. G. (1991). Is Subitizing A Unique Numerical Ability. *Perception & Psychophysics, 50,* 555-564.

Balakrishnan, J. D. & Ashby, F. G. (1992). Subitizing - Magical Numbers Or Mere Superstition. *Psychological Research-Psychologische Forschung, 54,* 80-90.

Balint, R. (1909). Paralysis of the soul "blindness", optic Ataxia, spatial disorder of Attention. *Monatsschrift fur Psychiatrie und Neurologie, 25,* 51-81.

Benton, A. L. (1977). Reflections on Gerstmann Syndrome. *Brain and Language, 4,* 45-62.

Berger, H. (1926). About acalulias with meningitis of the cerebrum. *Archiv fur Psychiatrie und Nervenkrankheiten, 78,* 238-263.

Bertelson, P. (1961). Sequential Redundancy and Speed in A Serial 2-Choice Responding Task. *Quarterly Journal of Experimental Psychology, 13,* 90-102.

Bertelson, P. (1965). Serial Choice Reaction-Time As A Function of Response Versus Signal-And-Response Repetition. *Nature, 206,* 217-&.

Biederman, I. (1972). Perceiving Real-World Scenes. *Science, 177,* 77-&.

Bundesen, C. (1990). A Theory of Visual-Attention. *Psychological Review, 97,* 523-547.

Butterworth, B. (1999). *The Mathematical Brain*. MacMillan, London.

Campbell, J. I. D. (1994). Architectures for Numerical Cognition. *Cognition, 53,* 1-44.

Campbell, J. I. D. & Clark, J. M. (1988). An Encoding-Complex View of Cognitive Number Processing - Comment. *Journal of Experimental Psychology-General, 117,* 204-214.

Campbell, J. I. D. & Epp, L. J. (2004). An encoding-complex approach to numerical cognition in Chinese-English bilinguals. *Canadian Journal of Experimental Psychology-Revue Canadienne de Psychologie Experimentale, 58,* 229-244.

Campbell, K. C. & Proctor, R. W. (1993). Repetition Effects with Categorizable Stimulus and Response Sets. *Journal of Experimental Psychology-Learning Memory and Cognition, 19,* 1345-1362.

Cantlon, J. F., Brannon, E. M., Carter, E. J., & Pelphrey, K. A. (2006). Functional imaging of numerical processing in adults and 4-y-old children. *Plos Biology, 4,* 844-854.

Castelli, F., Glaser, D. E., & Butterworth, B. (2006). Discrete and analogue quantity processing in the parietal lobe: A functional MRI study. *Proceedings of the National Academy of Sciences of the United States of America, 103,* 4693-4698.

Chong, S. C. & Treisman, A. (2003). Representation of statistical properties. *Vision Research, 43,* 393-404.

Chong, S. C. & Treisman, A. (2005). Attentional spread in the statistical processing of visual displays. *Perception & Psychophysics, 67,* 1-13.

Cinel, C. & Humphreys, G. W. (2006). On the relations between implicit and explicit spatial binding: Evidence from Balint's syndrome. *Cognitive Affective & Behavioral Neuroscience, 6,* 127-140.

Cipolotti, L. & Butterworth, B. (1995). Toward A Multiroute Model of Number Processing - Impaired Number Transcoding with Preserved Calculation Skills. *Journal of Experimental Psychology-General, 124,* 375-390.

Cipolotti, L., Butterworth, B., & Denes, G. (1991). A Specific Deficit for Numbers in A Case of Dense Acalculia. *Brain, 114,* 2619-2637.

Cohen, L. & Dehaene, S. (1995). Number processing in pure alexia: The effect of hemispheric asymmetries and task demands. *Neurocase, 1,* 121-137.

Cooper, A. C. G. & Humphreys, G. W. (2000). Coding space within but not between objects: evidence from Balint's syndrome. *Neuropsychologia, 38,* 723-733.

Corsi, P. M. (1972). Human memory and the medial temporal region of the brain. *Dissertation Abstracts International, 34* (02), 891B.

Coslett, H. B. & Saffran, E. (1991). Simultanagnosia - to See But Not 2 See. *Brain, 114,* 1523-1545.

Cowan, N. (2001). The magical number 4 in short-term memory: A reconsideration of mental storage capacity. *Behavioral and Brain Sciences, 24,* 87-+.

Crinion, J., Ashbumer, J., Leff, A., Brett, M., Price, C., & Friston, K. (2007). Spatial normalization of lesioned brains: Performance evaluation and impact on fMRI analyses. *Neuroimage, 37,* 866-875.

Dehaene, S. & Changeux, J. P. (1993). Development of Elementary Numerical Abilities - A Neuronal Model. *Journal of Cognitive Neuroscience, 5,* 390-407.

Dehaene, S. & Cohen, L. (1994). Dissociable Mechanisms of Subitizing and Counting - Neuropsychological Evidence from Simultanagnosic Patients. *Journal of Experimental Psychology-Human Perception and Performance, 20,* 958-975.

Dehaene, S. & Cohen, L. (1997). Cerebral pathways for calculation: Double dissociation between rote verbal and quantitative knowledge of arithmetic. *Cortex, 33,* 219-250.

Dehaene, S., Dehaene-Lambertz, G., & Cohen, L. (1998). Abstract representations of numbers in the animal and human brain. *Trends in Neurosciences, 21,* 355-361.

Dehaene, S., haene-Lambertz, G., & Cohen, L. (1998). Abstract representations of numbers in the animal and human brain. *Trends in Neurosciences, 21,* 355-361.

Dehaene, S., Piazza, M., Pinel, P., & Cohen, L. (2003). Three parietal circuits for number processing. *Cognitive Neuropsychology, 20,* 487-506.

Dehaene, S., Spelke, E., Pinel, P., Stanescu, R., & Tsivkin, S. (1999). Sources of mathematical thinking: Behavioral and brain-imaging evidence. *Science, 284,* 970-974.

Demeyere, N. & Humphreys, G. W. (2007). Distributed and Focused Attention: Neuropsychological Evidence for Separate Attentional Mechanisms when Counting and Estimating. J*ournal of Experimental Psychology-Human Perception and Performance* 33, 1076-1088.

Desimone, R., & Ungerleider, L. G. (1989). Neural mechanisms of visual processing in monkeys. In E. Boller & J. Grafman (Eds.), *Handbook of neuropsychology* (Vol. 2, pp. 267–299). Amsterdam: Elsevier.

Denys, K., Vanduffel, W., Fize, D., Nelissen, K., Peuskens, H., Van Essen, D. et al. (2004). The processing of visual shape in the cerebral cortex of human and nonhuman primates: A functional magnetic resonance imaging study. *Journal of Neuroscience, 24*, 2551-2565.

Duncan, J., Bundesen, C., Olson, A., Humphreys, G., Ward, R., Kyllingsbaek, S. et al. (2003). Attentional functions in dorsal and ventral simultanagnosia. *Cognitive Neuropsychology, 20,* 675-701.

Duvernoy, H.M., Cabanis, E.A., Vannson, J.L. (1991). *The Human brain surface, three-dimensional sectional anatomy and MRI*. Springer-Verlag; Wien.

Egeth, H. E., Leonard, C. J., & Palomares, M. (2008). The role of attention in subitizing: Is the magical number 1? *Visual Cognition, 16,* 463-473.

Feigenson, L., Dehaene, S., & Spelke, E. (2004). Core systems of number. *Trends in Cognitive Sciences, 8,* 307-314.

Forti, S. & Humphreys, G. W. (2004). Visuomotor cuing through tool use in unilateral visual neglect. *Journal of General Psychology, 131,* 379-410.

Freeman, E., Driver, J., Sagi, D., & Zhaoping, L. (2003). Top-down modulation of lateral interactions in early vision: Does attention affect integration of the whole or just perception of the parts? *Current Biology, 13,* 985-989.

Friedmanhill, S. R., Robertson, L. C., & Treisman, A. (1995). Parietal Contributions to Visual Feature Binding - Evidence from A Patient with Bilateral Lesions. *Science, 269,* 853-855.

Friston, K.J., Fletcher, P., Josephs, O., Holmes, A., Rugg, M., & Turner,R. (1998). Event-related fMRI: characterizing differential responses. *Neuroimage, 7*, 30-40.

Friston, K.J., Glaser, D.E., Mechelli, A., Turner, R., & Price,C. (2003). *Hemodynamic modeling.* In Human Brain Function, R.S. Frackowiak, K.J. Friston, C. Frith, R.J. Dolan, C. Price, S. Zeki, J. Ashburner, and W. Penny, eds. Academic Press), pp. 823-842.

Frith, U. (1989). *Autism: Explaining the Enigma*. Blackwell, Oxford.

Gallistel, C.R., & Gelman, R. (1991). *Subitizing: The preverbal counting process*. In F. Craik, W. Kessen, & A. Ortony (Eds.), Essays in honor of George Mandler (pp. 65–81). Erlbaum, Hillsdale, NJ.

Gallistel, C. R. & Gelman, R. (1992). Preverbal and Verbal Counting and Computation. *Cognition, 44,* 43-74.

Gelman, R. & Gallistel, C. R. (1978). *The child's understanding of number.* Harvard University Press, Oxford.

Gerstmann, J. (1940). Syndrome of finger agnosia, disorientation for right and left, agraphia and acalculia - Local diagnostic value. *Archives of Neurology and Psychiatry, 44,* 398-408.

Gilchrist, I. D., Humphreys, G. W., & Riddoch, M. J. (1996). Grouping and extinction: Evidence for low-level modulation of visual selection. *Cognitive Neuropsychology, 13,* 1223-1249.

Grabner, R. H., Ansari, D., Koschutnig, K., Reishofer, G., Ebner, F., & Neuper, C. (2009). To retrieve or to calculate? Left angular gyrus mediates the retrieval of arithmetic facts during problem solving. *Neuropsychologia, 47,* 604-608.

Grill-Spector, K., Kushnir, T., Edelman, S., Avidan, G., Itzchak, Y., & Malach, R. (1999). Differential processing of objects under various viewing conditions in the human lateral occipital complex. *Neuron, 24,* 187-203.

Gross, C. G. (1992). Representation of Visual-Stimuli in Inferior Temporal Cortex. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences, 335,* 3-10.

Halpern, C., Clark, R., Moore, P., Cross, K., & Grossman, M. (2007). Too much to count on: Impaired very small numbers in corticobasal degeneration. *Brain and Cognition, 64,* 144-149.

Hauser, M. D., MacNeilage, P., & Ware, M. (1996). Numerical representations in primates. *Proceedings of the National Academy of Sciences of the United States of America, 93,* 1514-1517.

Higgs, S., Williamson, A.C., Rotshtein, P., & Humphreys, G.W. (2008). Sensory-specific satiety is intact in amnesics who eat multiple meals. *Psychological Science, 19*, 623-628.

Himmelbach, M., Erb, M., Klockgether, T., Moskau, S., & Karnath, H. O. (2009). fMRI of global visual perception in simultanagnosia. *Neuropsychologia, 47,* 1173-1177.

Hochstein, S. & Ahissar, M. (2002). View from the top: Hierarchies and reverse hierarchies in the visual system. *Neuron, 36,* 791-804.

Holmes, G. (1918). Disturbances of visual orientation. *British Journal of Ophtalmology, 2,* 506-516.

Hulleman J., & Humphreys, G.W. (unpublished). Impaired tracking moving objects after damage to posterior parietal cortex.

Humphreys, G. W. (1998). Neural representation of objects in space: a dual coding account. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences, 353,* 1341-1351.

Humphreys, G. W., Cinel, C., Wolfe, J., Olson, A., & Klempen, N. (2000). Fractionating the binding process: neuropsychological evidence distinguishing binding of form from binding of surface features. *Vision Research, 40,* 1569-1596.

Humphreys, G. W. & Riddoch, M. J. (2003). From what to where: Neuropsychological evidence for implicit interactions between object- and space-based attention. *Psychological Science, 14,* 487-492.

Humphreys, G. W., Romani, C., Olson, A., Riddoch, M. J., & Duncan, J. (1994). Non Spatial Extinction Following Lesions of the Parietal Lobe in Humans. *Nature, 372,* 357-359.

Hyde, D. C. & Spelke, E. S. (2009). All Numbers Are Not Equal: An Electrophysiological Investigation of Small and Large Number Representations. *Journal of Cognitive Neuroscience, 21,* 1039-1053.

Intriligator, J. & Cavanagh, P. (2001). The spatial resolution of visual attention. *Cognitive Psychology, 43,* 171-216.

Julesz, B. (1984). Toward an axiomatic theory of preattentive vision. In EdelmanG.M., GallW.E., & CowanW.M. (Eds.), *Dynamic aspects of neocortical function* (pp. 585-612). New York: Wiley.

Kadosh, R. C., Kadosh, K. C., Kaas, A., Henik, A., & Goebel, R. (2007). Notation-dependent and -independent representations of numbers in the parietal lobes. *Neuron, 53,* 307-314.

Kadosh, R. C. & Walsh, V. (2007). Dyscalculia. *Current Biology, 17,* R946-R947.

Kadosh, R. C. & Walsh, V. (2009). Numerical representation in the parietal lobes: Abstract or not abstract? *Behavioral and Brain Sciences, 32,* 313-+.

Karnath, H. O., Ferber, S., Rorden, C., & Driver, J. (2000). The fate of global information in dorsal simultanagnosia. *Neurocase, 6,* 295-305.

Kaufman, E. L., Lord, M. W., Reese, T. W., & Volkmann, J. (1949). The Discrimination of Visual Number. *American Journal of Psychology, 62,* 498-525.

Kiebel, S., & Holmes, A. (2003). *The General Linear Model*. In Human Brain Function, R.S. Frackowiak, K.J. Friston, C. Frith, R.J. Dolan, C. Price, S. Zeki, J. Ashburner, and W. Penny, eds. Academic Press), pp. 725-760.

Kitadono, K. & Humphreys, G. W. (2007). Interactions between perception and action programming: Evidence from visual extinction and optic ataxia. *Cognitive Neuropsychology, 24,* 731-754.

Klein, R. M. (2000). Inhibition of return. *Trends in Cognitive Sciences, 4,* 138-147.

Kourtzi, Z. & Kanwisher, N. (2000). Cortical regions involved in perceiving object shape. *Journal of Neuroscience, 20,* 3310-3318.

Kourtzi, Z. & Kanwisher, N. (2001). Representation of perceived object shape by the human lateral occipital complex. *Science, 293,* 1506-1509.

Laeng, B., Kosslyn, S. M., Caviness, V. S., & Bates, J. (1999). Can deficits in spatial indexing contribute to simultanagnosia? *Cognitive Neuropsychology, 16,* 81-114.

Lassaline, M. E. & Logan, G. D. (1993). Memory-Based Automaticity in the Discrimination of Visual Numerosity. *Journal of Experimental Psychology-Learning Memory and Cognition, 19,* 561-581.

Lecerf, T. & de Ribaupierre, A. (2005). Recognition in a visuospatial memory task: The effect of presentation. *European Journal of Cognitive Psychology, 17,* 47-75.

Lemer, C., Dehaene, S., Spelke, E., & Cohen, L. (2003). Approximate quantities and exact number words: dissociable systems. *Neuropsychologia, 41,* 1942-1958.

Logan, G. D. & Zbrodoff, N. J. (2003). Subitizing and similarity: Toward a pattern-matching theory of enumeration. *Psychonomic Bulletin & Review, 10,* 676-682.

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

Mammarella, I. C., Cornoldi, C., Pazzaglia, F., Toso, C., Grimoldi, M., & Vio, C. (2006). Evidence for a double dissociation between spatial-simultaneous and spatial-sequential working memory in visuospatial (nonverbal) learning disabled children. *Brain and Cognition, 62,* 58-67.

Mandler, G. & Shebo, B. J. (1982). Subitizing - An Analysis of Its Component Processes. *Journal of Experimental Psychology-General, 111,* 1-22.

Mannan, S. K., Mort, D., Hodgson, T. L., Driver, J., Kennard, C., & Husain, M. (2005). Revisting previsously searched locations in visual neglect: Role of right parietal and frontal lesions in misjudging old locations as new (vol 17, pg 340, 2005). *Journal of Cognitive Neuroscience, 17,* CP1.

Mayer, E., Martory, M. D., Pegna, A. J., Landis, T., Delavelle, J., & Annoni, J. M. (1999). A pure case of Gerstmann syndrome with a subangular lesion. *Brain, 122,* 1107-1120.

Mccloskey, M. (1992). Cognitive Mechanisms in Numerical Processing - Evidence from Acquired Dyscalculia. *Cognition, 44,* 107-157.

Mccloskey, M., Caramazza, A., & Basili, A. (1985). Cognitive Mechanisms in Number Processing and Calculation - Evidence from Dyscalculia. *Brain and Cognition, 4,* 171-196.

Mcfie, J., Piercy, M. F., & Zangwill, O. L. (1950). Visual-Spatial Agnosia Associated with Lesions of the Right Cerebral Hemisphere. *Brain, 73,* 167-190.

Mori, S. (2005). *MRI atlas of human white matter*. Elsevier, Amsterdam.

Navon, D. (1977). Forest Before Trees - Precedence of Global Features in Visual-Perception. *Cognitive Psychology, 9,* 353-383.

Noel, M. P. & Seron, X. (1993). Arabic Number Reading Deficit - A Single-Case Study Or When 236 Is Read (2306) and Judged Superior to 1258. *Cognitive Neuropsychology, 10,* 317-339.

Olivers, C. N. L. & Watson, D. G. (2008). Subitizing requires attention. *Visual Cognition, 16,* 439-462.

Palmeri, T. J. (1997). Exemplar similarity and the development of automaticity. *Journal of Experimental Psychology-Learning Memory and Cognition, 23,* 324-354.

Parkes, L., Lund, J., Angelucci, A., Solomon, J. A., & Morgan, M. (2001). Compulsory averaging of crowded orientation signals in human vision. *Nature Neuroscience, 4,* 739-744.

Pashler, H. & Baylis, G. (1991). Procedural Learning .2. Intertrial Repetition Effects in Speeded-Choice Tasks. *Journal of Experimental Psychology-Learning Memory and Cognition, 17,* 33-48.

Piazza, M., Giacomini, E., Le Bihan, D., & Dehaene, S. (2003). Single-trial classification of parallel pre-attentive and serial attentive processes using functional magnetic resonance imaging. *Proceedings of the Royal Society of London Series B-Biological Sciences, 270,* 1237-1245.

Piazza, M., Izard, V., Pinel, P., Le Bihan, D., & Dehaene, S. (2004). Tuning curves for approximate numerosity in the human intraparietal sulcus. *Neuron, 44,* 547-555.

Piazza, M., Mechelli, A., Butterworth, B., & Price, C. J. (2002). Are subitizing and counting implemented as separate or functionally overlapping processes? *Neuroimage, 15,* 435-446.

Piazza, M., Mechelli, A., Price, C. J., & Butterworth, B. (2006). Exact and approximate judgements of visual and auditory numerosity: An fMRI study. *Brain Research, 1106,* 177-188.

Piazza, M., Pinel, P., Le Bihan, D., & Dehaene, S. (2007). A magnitude code common to numerosities and number symbols in human intraparietal cortex. *Neuron, 53,* 293-305.

Pillon, A. & Pesenti, M. (2001). Calculating without reading? Comments on Cohen and Dehaene (2000). *Cognitive Neuropsychology, 18,* 275-284.

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

Pylyshyn, Z. (1989). The Role of Location Indexes in Spatial Perception - A Sketch of the Finst Spatial-Index Model. *Cognition, 32,* 65-97.

Pylyshyn, Z. W. & Storm, R. W. (1988). Tracking Multiple Independent Targets Evidence for A Parallel Tracking Mechanism. *Spatial Vision, 3,* 179-198.

Rabbitt, P. M. A. (1968). Repetition Effects and Signal Classification Strategies in Serial Choice-Response Tasks. *Quarterly Journal of Experimental Psychology, 20,* 232-&.

Railo, H., Koivisto, M., Revonsuo, A., & Hannula, M. M. (2008). The role of attention in subitizing. *Cognition, 107,* 82-104.

Rensink, R. A. & Enns, J. T. (1995). Preemption Effects in Visual-Search - Evidence for Low-Level Grouping. *Psychological Review, 102,* 101-130.

Revkin, S. K., Piazza, M., Izard, V., Cohen, L., & Dehaene, S. (2008). Does subitizing reflect numerical estimation? *Psychological Science, 19,* 607-614.

Riddoch, M. J., Humphreys, G. W., Jacobson, S., Pluck, G., Bateman, A., & Edwards, M. (2004). Impaired orientation discrimination and localisation following parietal damage: On the interplay between dorsal and ventral processes in visual perception. *Cognitive Neuropsychology, 21,* 597-623.

Riddoch, M.J., Chechlasz, M., Mevorach, C., Mavritsaki, E., Allen, H.A., and Humphreys, G.W. (in press). *Annual Reviews in Neuroscience.*

Robertson, I.H., Ward, T., Ridgeway, V. & Nimmo-Smith, I. (1991) *The Test of Everyday Attention (TEA).* Bury St. Edmonds: Thames Valley Test Company.

Rusconi, E., Pinel, P., Eger, E., Lebihan, D., Thirion, B., Dehaene, S. et al. (2009). A Disconnection Account of Gerstmann Syndrome: Functional Neuroanatomy Evidence. *Annals of Neurology, 66,* 654-662.

Sathian, K., Simon, T. J., Peterson, S., Patel, G. A., Hoffman, J. M., & Grafton, S. T. (1999). Neural evidence linking visual object enumeration and attention. *Journal of Cognitive Neuroscience, 11,* 36-51.

Schneider, Z., Eschman, A., & Zuccolotto, A. (2002). E-Prime (Version 1) [Computer software]. Pittsburgh, PA: Psychology Software Tools.

Schwarz, W. & Ischebeck, A. (2003). On the relative speed account of number-size interference in comparative judgments of numerals. *Journal of Experimental Psychology-Human Perception and Performance, 29,* 507-522.

Seron, X., Deloche, G., Ferrand, I., Cornet, J. A., Frederix, M., & Hirsbrunner, T. (1991). Dot Counting by Brain-Damaged Subjects. *Brain and Cognition, 17,* 116-137.

Shalev, L. & Humphreys, G. W. (2002). Implicit location encoding via stored representations of familiar objects: Neuropsychological evidence. *Cognitive Neuropsychology, 19,* 721-744.

Shalev, L., Humphreys, G. W., & Mevorach, C. (2005). Global processing of compound letters in a patient with Balint's syndrome. *Cognitive Neuropsychology, 22,* 737-751.

Shulman, G. L., Astafiev, S. V., Mcavoy, M. P., Davossa, G., & Corbetta, M. (2007). Right TPJ deactivation during visual search: Functional significance and support for a filter hypothesis. *Cerebral Cortex, 17,* 2625-2633.

Shuman, M. & Kanwisher, N. (2004). Numerical magnitude in the human parietal lobe: Tests of representational generality and domain specificity. *Neuron, 44,* 557-569.

Simon, T. J. & Vaishnavi, S. (1996). Subitizing and counting depend on different attentional mechanisms: Evidence from visual enumeration in afterimages. *Perception & Psychophysics, 58,* 915-926.

Smith, M. C. (1968). Repetition Effect and Short-Term Memory. *Journal of Experimental Psychology, 77,* 435-&.

Stamatakis, E. A. & Tyler, L. K. (2005). Identifying lesions on structural brain images - Validation of the method and application to neuropsychological patients. *Brain and Language, 94,* 167-177.

Thaiss, L. & Debleser, R. (1992). Visual Agnosia - A Case of Reduced Attentional Spotlight. *Cortex, 28,* 601-621.

Thorpe, S., Fize, D., & Marlot, C. (1996). Speed of processing in the human visual system. *Nature, 381,* 520-522.

Todd, J. J. & Marois, R. (2004). Capacity limit of visual short-term memory in human posterior parietal cortex. *Nature, 428,* 751-754.

Torralba, A., Oliva, A., Castelhano, M. S., & Henderson, J. M. (2006). Contextual guidance of eye movements and attention in real-world scenes: The role of global features in object search. *Psychological Review, 113,* 766-786.

Townsend, J. T. & Ashby, F. G. (1983). *Stochastic modelling of elementary psychological processes.* Cambridge University Press.

Treisman, A. (1998). Feature binding, attention and object perception. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences, 353,* 1295-1306.

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

Treisman, A. M. & Gelade, G. (1980). Feature-Integration Theory of Attention. *Cognitive Psychology, 12,* 97-136.

Trick, L. & Pylyshyn, Z. (1989). Subitizing and the Finst Spatial Index Model. *Bulletin of the Psychonomic Society, 27,* 490.

Trick, L. M. & Pylyshyn, Z. W. (1993). What Enumeration Studies Can Show Us About Spatial Attention - Evidence for Limited Capacity Preattentive Processing. *Journal of Experimental Psychology-Human Perception and Performance, 19,* 331-351.

Trick, L. M. & Pylyshyn, Z. W. (1994). Why Are Small and Large Numbers Enumerated Differently - A Limited-Capacity Preattentive Stage in Vision. *Psychological Review, 101,* 80-102.

Tuholski, S. W., Engle, R. W., & Baylis, G. C. (2001). Individual differences in working memory capacity and enumeration. *Memory & Cognition, 29,* 484-492.

Tyler, L. K. & Stamatakis, E. A. (2005). Differentiating lexical form, meaning and structure in the language system: A voxel based correlational study. *Journal of Cognitive Neuroscience,* 79.

Tyler, L.K., Marslen-Wilson, W., & Stamatakis, E.A. (2005). Dissociating neuro-cognitive component processes: voxel-based correlational methodology. *Neuropsychologia, 43,* 771-778.

Tyler, L.K., Shafto, M.A., Randall, B., Wright, P., Marslen-Wilson, W.D., & Stamatakis,E.A. (2009). *Preserving Syntactic Processing across the Adult Life Span: The Modulation of the Frontotemporal Language System in the Context of Age-Related Atrophy.* Cerebral Cortex., *20,* 352-364.

Tyler, L.K., Stamatakis, E.A., Bright, P., Acres, K., Abdallah, S., Rodd, J.M., & Moss, H.E. (2004). Processing objects at different levels of specificity. *Journal of Cognitive Neuroscience, 16*, 351-362.

Vanoeffelen, M. P. & Vos, P. G. (1982). A Probabilistic Model for the Discrimination of Visual Number. *Perception & Psychophysics, 32,* 163-170.

Vetter, P., Butterworth, B., & Bahrami, B. (2008). Modulating attentional load affects numerosity estimation: evidence against a pre-attentive subitizing mechanism. *Plos One, 3,* e3269.

Vuilleumier, P. & Rafal, R. (1999). "Both" means more than "two": localizing and counting in patients with visuospatial neglect. *Nature Neuroscience, 2,* 783-784.

Vuilleumier, P. O. & Rafal, R. D. (2000). A systematic study of visual extinction - Between- and within-field deficits of attention in hemispatial neglect. *Brain, 123,* 1263-1279.

Warrington, E. K. & James, M. (1967). Tachistosocpic Number Estimation in Patients with Unilateral Cerebral Lesions. *Journal of Neurology Neurosurgery and Psychiatry, 30,* 468-&.

Watson, D. G. & Humphreys, G. W. (1999). The magic number four and temporo-parietal damage: Neurological impairments in counting targets amongst distractors. *Cognitive Neuropsychology, 16,* 609-629.

Watson, D. G. & Maylor, E. A. (2006). Effects of colour heterogeneity on subitization. *Perception & Psychophysics, 68,* 319-326.

Watson, D. G., Maylor, E. A., & Bruce, L. A. M. (2005). The efficiency of feature-based subitization and counting. *Journal of Experimental Psychology-Human Perception and Performance, 31,* 1449-1462.

Watson, D. G., Maylor, E. A., & Bruce, L. A. M. (2007). The role of eye movements in subitizing and counting. *Journal of Experimental Psychology-Human Perception and Performance, 33,* 1389-1399.

Watson, D. G., Maylor, E. A., & Manson, N. J. (2002). Aging and enumeration: A selective deficit for the subitization of targets among distractors. *Psychology and Aging, 17,* 496-504.

Wilson, B., Cockburn, J. and Halligan, P. (1985) *The Behavioral Inattention Test* Thames Valley Test Company , Flempton

Wojciulik, E., Husain, M., Clarke, K., & Driver, J. (2001). Spatial working memory deficit in unilateral neglect. *Neuropsychologia, 39,* 390-396.

Wolfe, J. M. (1998). What can 1 million trials tell us about visual search? *Psychological Science, 9,* 33-39.

Wolters, G., Vankempen, H., & Wijlhuizen, G. J. (1987). Quantification of Small Numbers of Dots - Subitizing Or Pattern-Recognition. *American Journal of Psychology, 100,* 225-237.

Worsley, K.J. (2003). Developments in random field theory. In: Frackowiak RSJ, Friston KJ, Frith C *et al*, editors. Human Brain Function. Academic Press, 881-886.

Xu, Y. D. & Chun, M. M. (2006). Dissociable neural mechanisms supporting visual short-term memory for objects. *Nature, 440,* 91-95.

Xu, Y. D. & Chun, M. M. (2009). Selecting and perceiving multiple visual objects. *Trends in Cognitive Sciences, 13,* 167-174.

Zhang, W. W. & Luck, S. J. (2008). Discrete fixed-resolution representations in visual working memory. *Nature, 453,* 233-235.

APPENDIX 1:

JOURNAL OF EXPERIMENTAL PSYCHOLOGY:

HUMAN PERCEPTION AND PERFORMANCE, 33, 1076-1088

(2007)

APPENDIX 2:

NEUROPSYCHOLOGIA, 46, 2861-2864 (2008)

APPENDIX 3:

NEUROCASE, IN PRESS (2010)