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'What' and 'Where' in the Intraparietal Sulcus:
An fMRI Study of Object Identity and Location in Visual Short-Term Memory

par
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Mémoire présenté à la Faculté des études supérieures
en vue de l'obtention du grade de M.Sc. en psychologie

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Faculté des études supérieures

Ce mémoire intitulé :

‘What’ and ‘Where’ in the Intraparietal Sulcus:
An fMRI Study of Object Identity and Location in Visual Short-Term Memory

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Le sillon intra-pariétal (SIP) a déjà été relié aux limitations de la mémoire visuelle à court-terme (MVCT, Todd & Marois, 2004). Par contre on ne sait pas si l'activation du SIP pendant les tâches de MVCT reflète la mémoire pour l'identité des objets ou pour leurs localisations dans l'espace. La présente étude a été conçue pour manipuler sélectivement la quantité d'information spatiale relative à l'identité retenue en MVCT afin de déterminer, à l'aide de l'imagerie par résonance magnétique fonctionnelle, l'effet de charge de chaque type d'information sur l'activation du SIP. Les résultats ont démontré une augmentation d'activité dans le SIP seulement pour une augmentation de charge mnésique spatiale. La charge mnésique d'identité n'avait aucun effet et il n'y avait pas d'interaction entre les deux types d'information. Ces résultats suggèrent que l'activation liée à la capacité de la MVCT observée antérieurement reflète d'abord la quantité d'information spatiale retenue en MVCT.

Mots clés: capacité; charge mnésique; cortex pariétal; mémoire de travail; mémoire à court-terme; mémoire spatiale; neuroimagerie

The intra-parietal sulcus (IPS) has been closely linked to limitations on visual short-term memory (VSTM, Todd & Marois, 2004). It is not known, however, whether IPS activation reflects VSTM for object identity or spatial location information. The present study was designed to manipulate selectively the amount of object identity and location information, or ‘What’ and ‘Where’, retained in VSTM in order to determine the effect of load for each type of VSTM on IPS activation, using functional magnetic resonance imaging. Results from 14 subjects showed an increase in IPS activation only in response to increasing Where memory load, with no effect of What load and no interaction. This suggests that capacity-related activation in the IPS primarily reflects the amount of spatial information retained in VSTM.

Keywords: capacity; memory load; parietal cortex; neuroimaging; short-term memory; spatial memory; working memory

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List of Abbreviations

BOLD: blood oxygen level dependent

CTE: cluster threshold estimation

fMRI: functional magnetic resonance imaging

IOS: intraoccipital sulcus

IPS: intraparietal sulcus

SPM: statistical parametric map

TR: repetition time

VOI: volume(s) of interest

VSTM: visual short-term memory

WM: working memory

Introduction

Working memory (WM) is a limited-capacity system that maintains information in an active, rapidly accessible state for a brief period of time. It allows the manipulation and integration of information from various sources that is necessary for complex cognitive tasks like language comprehension, learning, and reasoning. According to Baddeley's widely accepted model (Baddeley & Hitch, 1974; Baddeley, 1992a; 1992b) working memory can be divided into three dissociable but complementary subsystems. The central executive serves as an attentional control system and coordinates information from the verbal and visuospatial WM systems. Verbal working memory, also called the phonological loop, stores acoustic or speech-based information and maintains it using subvocal repetition. Visual working memory, also known as the visuospatial sketchpad, briefly stores information about visual objects and their spatial properties. Converging evidence from behavioural, neuroimaging, and clinical neuropsychological studies supports the independence of verbal and visual working memory (e.g., Baddeley & Hitch, 1974; Hartley & Speer, 2000; Smith & Jonides, 1998; Wang & Bellugi, 1994). Verbal and visuospatial WM can each be further subdivided into storage and manipulation components (Smith & Jonides, 1998; 1999). It is the storage component of visuospatial working memory that forms the topic of the present thesis, and will henceforth be referred to as visual short-term memory (VSTM).

Perhaps the most defining feature of VSTM is its extremely limited capacity. Despite our rich visual experience, our capacity to retain visual information extends to only 3 or 4 items at a time (Luck & Vogel, 1997; Vogel, Woodman & Luck, 2001). In a seminal study, Luck and Vogel (1997) used a delayed match-to-sample task to examine VSTM capacity for single-feature objects and for conjunctions of features. In each trial, participants were shown a sample array and a test array, separated by a 900 ms retention interval, and were asked to indicate whether the arrays were identical or whether they differed in terms of a single feature. The first experiment examined VSTM for simple colours. The memory arrays consisted of 1-12 coloured squares. Performance was near ceiling for set sizes 1-3, but declined systematically thereafter. The number of objects stored in VSTM was estimated using Cowan's K formula (Pashler, 1988; Cowan, 2001):

$$K = N (\textit{hit rate} + \textit{correct rejection rate} - 1)$$

where K is the number of objects in VSTM and N is the number of objects in the sample array. According to estimates of K , participants were able to retain approximately four coloured squares in memory. The influence of verbal working memory, perceptual encoding limitations, and decision factors on performance were ruled out by adding an articulatory control task, varying stimulus duration, and using a cued partial-report procedure, respectively. None of the above factors affected performance on the colour VSTM task. The next experiment examined VSTM capacity for different features and for conjunctions of features. The procedure was similar to the colour-only VSTM task, but the stimuli in this case were coloured, oriented bars. Participants were required to remember either colour, orientation, or both, depending on

the condition. Performance was nearly identical for colour and orientation, with a capacity of about four items for both feature types. Interestingly, this result did not change when participants were required to remember both colour and orientation, suggesting that the stimuli were stored as integrated objects rather than individual features. However, it is also possible that participants were unable to avoid encoding the irrelevant stimulus dimension in the single feature condition. In order to address this potential explanation for the lack of differences in performance between the single feature and conjunction conditions, a second version of the experiment was performed where the irrelevant stimulus dimension in the single-feature conditions was held constant (i.e., all the bars were black in the orientation condition, and all were vertical in the colour condition). The finding of statistically identical performance between single feature and conjunction conditions remained unchanged. Performance remained the same, even when each object was defined by a conjunction of 4 features: colour, orientation, size, and presence or absence of a gap. Together, the findings from Luck and Vogel (1997) suggest that approximately four integrated objects can be successfully stored in VSTM at any given time.

Luck and Vogel's (1997) finding was advanced by Vogel and Machizawa (2004) who took advantage of the contralateral organization of the visual system by presenting lateralized stimuli, so that spatially specific hemispheric VSTM responses could be measured using event-related potentials (ERP). They found a large negativity over contralateral posterior parietal and occipital electrode sites that persisted throughout the retention interval of each trial. The amplitude of the negativity was highly sensitive to

number of items in the array and was smaller for incorrect than correct trials. Despite decreasing accuracy for supra-capacity arrays, the amplitude of the contralateral delay activity did not change between capacity and supra-capacity arrays, but the increase in amplitude between 2 and 4 items was strongly correlated with individual VSTM capacity. This effect was not simply due to task difficulty since the amplitude of the negativity did not increase once VSTM capacity was reached, while accuracy continued to decrease. Together the results of this study suggested that the observed contralateral delay activity indexed the number of active representations successfully retained in VSTM.

At the same time Vogel and Machizawa's (2004) electrophysiological study of VSTM capacity was published, Todd and Marois (2004) published an fMRI study using a similar parametric load manipulation paradigm that investigated the neural locus of VSTM capacity constraints. Each trial consisted of a sample display containing one, two, three, four, six, or eight coloured discs arranged in nine possible locations on an invisible 3×3 matrix presented for 150 ms. The sample display was followed by a 1200 ms retention interval and a 1750 ms probe display containing one coloured disc at one of the previously occupied locations. Subjects indicated by button press whether the probe disc matched the sample disc for that location. In order to minimize verbal recoding, an articulatory suppression task was performed concurrently. Each trial started with an auditory presentation of two digits that were to be rehearsed throughout the trial. Following the probe display and response, two digits were presented visually and participants indicated by button press whether they matched the rehearsed digits.

Performance on the verbal task was uniformly high, and was independent of VSTM load. The absence of a trade-off between visual and verbal task performance suggested that participants were not using a verbal recoding strategy in the VSTM task. Because of this finding, and the analogous finding in Luck and Vogel (1997), an articulatory suppression task was deemed unnecessary for the study to be presented in the current thesis. Accuracy in the VSTM task declined in a linear fashion with increasing set size whereas the number of objects retained in VSTM, as estimated using Cowan's K , increased only up to set size 3 or 4 before levelling off. This is consistent with the studies outlined above, as was the finding that capacity estimates were not affected when stimulus duration was increased from 150 ms to 450 ms, and therefore not limited by perception or encoding processes.

Brain regions that are related to VSTM capacity should show blood-oxygen level dependent (BOLD) responses that parallel the behavioural K -function, increasing up to set size 3 or 4 and then levelling off. In order to identify these regions, a whole-brain voxelwise multiple regression was performed on the fMRI data, using K -weighted set size coefficients. The result was a single, bilateral region in the intraparietal and intraoccipital sulci (IPS/IOS). A time course analysis confirmed that the peak BOLD response in this region, like the K -function, increased only up to set size 4. It is important to remember that this result cannot be due to task difficulty since accuracy continued to decrease and reaction times continued to increase beyond set size 4, while K estimates and IPS/IOS BOLD activation did not. The result was also not caused by perceptual or iconic representation of the sample array, since an iconic memory

experiment which required an immediate judgement as to the presence or absence of a coloured disc in the centre of the array showed an overall lower BOLD signal in the IPS/IOS that was insensitive to set size.

In order to conclude that the IPS/IOS is implicated in VSTM storage capacity, it must be shown that *K*-related activity is present during the maintenance phase of the memory task, and not just during encoding or retrieval. Because of the nature of the haemodynamic response, the short retention interval used in the above experiment did not permit separation of activation into encoding, maintenance, and retrieval. To address this issue, Todd and Marois (2004) designed a second fMRI experiment using a slow event-related paradigm. Trials were the same as the first experiment, except that the retention interval was extended to 9200 ms and only set sizes 1 and 3 were used in order to compensate for the smaller number of trials acquired. IPS/IOS activation during the slow event-related task was higher for set size 3 than for set size 1 during encoding and maintenance, but not during retrieval, supporting the idea that IPS/IOS is a key neural locus of capacity-limited VSTM storage processes.

In a follow-up study (Todd & Marois, 2005), the relationship between individual differences in VSTM capacity and IPS/IOS activation was examined. This was motivated by the observation of considerable variability in individual VSTM capacity, with *K* values ranging between 1.74 and 6.37 in the Todd and Marois (2004) sample. Since the group average analysis used in Todd and Marois (2004) treated intersubject variability as error, it could not inform as to the neural bases of individual differences. If the IPS/IOS activation that was observed with the group analysis did not prove to be

related to individual differences in performance, it would weaken the argument that the IPS/IOS is instrumental in determining VSTM capacity and suggest a more generic contribution to VSTM processing with other regions perhaps accounting for individual variability. If, however, it can be shown that the IPS/IOS is not only activated in a significant proportion of subjects but that it can also account for intersubject variability in performance, a strong case can be made for the role of the IPS/IOS in regulating VSTM capacity.

For each subject, the maximum number of items that could be stored in VSTM (K_{max}) was determined as well as the percent BOLD signal change relative to no-event signal at that set size. BOLD activity levels were standardized across individuals by subtracting activity at set size 1 from activity at K_{max} , since subjects had virtually identical K -values at set size 1 but very different BOLD signal levels. For each individual, regressors were defined for set sizes 1 and K_{max} and weighted by the subject's maximum K value. Voxel based analysis was then performed to identify voxels whose activity covaried with the magnitude of difference between set size 1 and set size K_{max} across individuals.

The resulting statistical parametric map (SPM) revealed a single region whose activity correlated with individual differences in VSTM capacity, located in the left IPS/IOS and largely overlapping with the region identified in Todd and Marois (2004). The right IPS/IOS was also correlated with individual differences when the stringent statistical threshold was reduced tenfold. This result suggests that not only is the

IPS/IOS involved in general capacity-related VSTM processes, but that it also plays an active role in determining individual performance.

The Todd and Marois (2004; 2005) studies have established the IPS/IOS as a key neural locus of limitations on VSTM capacity on both a group and individual level. One question that remains, however, is what type of visual information is indexed by the IPS/IOS during VSTM tasks. One characteristic of the delayed match-to-sample paradigms used in Todd and Marois' investigations of VSTM is that each object in the memory array occupied a distinct spatial location. In order to successfully perform the task, participants had to retain both the colour of the object and its location in space. It is possible therefore, that the IPS/IOS represents location, colour, or an integrated representation of both. Todd and Marois (2004) briefly addressed this issue by performing an additional experiment using a paradigm identical to that of the first experiment, except that the test stimulus was always presented at fixation, rendering location information irrelevant to the task. The load dependent, *K*-correlated BOLD response function was still observed in the IPS/IOS and the authors concluded that the IPS/IOS was therefore not involved uniquely in location processing. It is not clear however, that the presentation of the probe stimulus at fixation would prevent the encoding and maintenance of location information during the retention interval. Participants were not instructed to ignore location, and the sample array still contained both colour and location information. It is possible that observers were still encoding both stimulus dimensions regardless of their necessity for the task.

Xu and Chun (2006) also examined the object identity versus location issue in their study of object complexity on IPS activation in VSTM tasks. The VSTM paradigm was similar to Todd and Marois' (2004) except that black shapes were used instead of coloured discs. Xu and Chun's manipulation of identity versus location information involved three presentation conditions: sequential centred (at fixation), sequential off-centre, and simultaneous off-centre. The probe object was always presented at fixation, rendering location unnecessary to successful task performance. No behavioural differences were observed between presentation conditions. Activation in the superior IPS varied with set size and correlated with K in all conditions, but inferior IPS exhibited this activation pattern only when objects appeared at different locations, i.e., in the sequential off-centre and simultaneous off-centre conditions. The authors conclude that the superior IPS indexes both object identity and location while the inferior IPS indexes object locations only.

There are several aspects of this experiment that make Xu and Chun's conclusions debatable. First of all, by the authors' own logic, observers should not be making use of location information to perform the task in any of the three conditions, yet the authors conclude that differences in inferior IPS between conditions are due to the encoding of location. Secondly, even if location was encoded by participants, none of the conditions can be directly compared to test for differences between same and different locations – the sequential centred and sequential off-centre conditions confound location with stimulus eccentricity, the sequential centred and simultaneous off-centre conditions again differ in stimulus eccentricity, but also in presentation rate

(simultaneous or one at a time), and the sequential and simultaneous off-centre conditions can only inform us of differences related to presentation rate.

Previous methodological difficulties made it necessary to design an experiment to specifically test the effects of VSTM for object identity and location on IPS/IOS activation. Because it is unclear whether participants are able to encode selectively colour, location, or both, the paradigm must include a parametric manipulation of each dimension independently, without requiring subjects to ignore one or the other. It was with this goal in mind that the present study was undertaken. The following article relates the experiment in detail.

**‘What’ and ‘Where’ in the Intraparietal Sulcus:
An fMRI Study of Object Identity and Location in Visual Short-Term Memory**

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The candidate, Amabilis Harrison, was responsible for all data collection, data analysis, and the writing of the scientific article. The co-authors provided guidance for the experimental design and feedback on the manuscript.

Many everyday cognitive functions require the ability to retain visual information in an active and readily accessible store for a short time. Our capacity to do so, however, is surprisingly limited, considering the rich and complex visual world we experience. In fact, the maximum number of items that can be retained in visual short-term memory (VSTM) at any given time is 3 or 4 (Luck and Vogel, 1997; Vogel, Woodman, and Luck, 2001). Investigations of the neural substrates of VSTM have revealed a large functional network in the lateral prefrontal and parietal cortices (Courtney, Ungerleider, Keil, and Haxby, 1997; D'Esposito, Aguirre, Zarahn, Ballard, Shin, and Lease, 1998; Postle and D'Esposito, 1999; Haxby, Petit, Ungerleider, and Courtney, 2000; Postle, Stern, Rosen and Corkin, 2000; Munk et al., 2002; Pessoa, Gutierrez, Bandettini, and Ungerleider, 2002; Linden et al., 2003; Sala, Rämä, and Courtney, 2003; Sala and Courtney, 2007). However, only a few studies have explored the neural bases of the strict limitations on VSTM capacity (Todd and Marois, 2004; 2005; Vogel and Machizawa, 2004; Xu and Chun, 2006). Todd and Marois (2004) identified a region in the posterior parietal cortex where activation levels during a VSTM task were tightly correlated with behavioural measures of VSTM capacity. As the number of items to be remembered increased from 1 to 8, both the number of items successfully maintained in VSTM — as estimated using Cowan's K formula (Pashler, 1988; Cowan, 2001) — and the BOLD fMRI signal in the intra-parietal and intra-occipital sulci (IPS/IOS) increased up to set size 3 or 4 but levelled off thereafter. The argument that the IPS/IOS is a key locus of VSTM storage capacity was further

strengthened by an individual-differences analysis (Todd and Marois, 2005) that revealed that IPS/IOS activity predicts *individual* VSTM storage capacity.

Todd and Marois' (2004; 2005) findings are consistent with an electrophysiological study that observed a lateralized event-related potential (ERP) response over posterior parieto-occipital sites that was strongly modulated by the number of visual objects retained in memory, and that reached asymptote at each subject's individual VSTM capacity (Vogel and Machizawa, 2004). One question that remains unanswered is what kind of information is indexed by the capacity-related activation in the IPS/IOS. In the Todd and Marois experiments, subjects retained both the identity (color) and location of objects in the memory array. Behavioural evidence suggests that VSTM stores for object identity and location are dissociable (Vuontela, Rämä, Raninen, Aronen, and Carlson, 1999; Lee and Chun, 2000; Klauer and Zhao, 2004), and several neuroimaging studies have observed a dorsal-ventral dissociation between spatial and object working memory processing streams (Courtney, Ungerleider, Keil, and Haxby, 1996; Munk et al., 2002; Sala et al., 2003; Mohr, Goebel, and Linden, 2006). It is therefore reasonable to expect that the capacity-related activation in the IPS/IOS may primarily reflect VSTM storage of location, or that sub-regions within the IPS/IOS may be dissociable according to identity and location representation.

Previous attempts to disentangle the influence of 'What' and 'Where' in the IPS/IOS have either relied on instructions to ignore one of the two stimulus dimensions (Todd and Marois, 2004), which has been shown to attenuate dissociations between domain-specific activations (Postle et al., 2000), or have confounded location

information with stimulus presentation parameters such as eccentricity and presentation rate (Xu and Chun, 2006, see discussion), leading to multiple possible interpretations of the results. Consequently, the precise role of the IPS/IOS with regards to the What-versus-Where issue is unclear and further research is required to understand exactly the function of the IPS/IOS in VSTM tasks.

The present study employed a novel method to dissociate memory for What and Where using simple visual stimuli. Doing so is generally not straightforward because most simple stimuli (e.g., coloured discs) convey information about both What (i.e., colour) and Where (i.e., the location occupied by the stimulus). Furthermore, the typical delayed match-to-sample task can be performed successfully by remembering both content and location of each item. The current approach was to present three coloured discs sequentially, and to vary the number of colours in the sequence, the number of locations, or both. By presenting these various alternatives in distinct blocks of trials, subjects were more likely to encode only the distinct colours, distinct locations, or both, depending on the experimental condition in that block of trials. There were four conditions — What1-Where1, What3-Where1, What1-Where3, and What3-Where3 — that represented the orthogonal manipulation of memory load for What (1 vs. 3) and memory load for Where (1 vs. 3) (Figure 2). Consider first the What3-Where1 condition, in which three disks of different colours (e.g., red, yellow, and green) were presented sequentially at the same location. In this block of trials, subjects knew that every trial would consist of three distinct colours presented at one location (at the beginning of the trial, the particular location was not known, but this became evident

with the presentation of the first disc). Relative to the What3-Where1, the What1-Where1 condition required only encoding a single colour, while providing a control for the amount of information about Where (always 1 in these blocks). If IPS/IOS stores information about spatial location, but not colour, then the activation in this region should be comparable in these two conditions. If, in contrast, IPS/IOS stores information about object identity (colour, in this case), then the region should be more active in the What3-Where1 condition than in the What1-Where1 condition. Similarly, the What1-Where3 condition increased load for spatial location while keeping load for content/colour constant, relative to the What1-Where1 condition. The What3-Where3 condition represented the high load condition in both dimensions and provided additional anchor points for the 2 by 2 design. Thus, the experimental design employed stimuli designed to vary memory load independently in terms of What information (by varying the number of distinct colours to remember) and Where information (by varying the number of different spatial locations to remember). Furthermore, the blocked presentation of the various memory-load conditions was designed to emphasize to subjects that the number of colours and locations would not vary within blocks. Given that maintaining information in VSTM is an effortful and capacity limited process (e.g., Stevanovski and Jolicœur, 2007), it was anticipated that subjects would minimize the processing required to succeed in the task by anticipating the same number of colours and locations in all trials within a block. Finally, a critical aspect of the stimuli was that the number of presented discs was the same in all conditions and the retinal eccentricity of the stimuli were always the same. These aspects of the experimental design

minimized stimulation differences across conditions, allowing us to interpret activation differences in terms of varying memory loads in the What versus Where dimensions.

Materials and Methods

Participants

Twenty Université de Montréal students (7 male, 13 female, ages 20-31) participated for financial compensation. All had normal or corrected to normal visual acuity and colour vision and had no history of neurological disease or disorder. Written informed consent was obtained prior to testing. The research protocol was approved by the research ethics committee of the Regroupement Neuroimagerie du Québec at the University of Montreal.

Task Design

The experiment was composed of two separate tasks. The first task used a fast event-related design to localize the IPS/IOS and was modelled after the delayed match-to-sample task used by Todd and Marois (2004). In each trial (Figure 1), a fixation cross was presented for 500 ms followed by an array of 1, 2, 3, or 5 coloured discs, each in a different colour (red, blue, green, orange, yellow, or pink). The discs were presented at 6 possible locations on an invisible circle around fixation for 200 ms. After a 1500 ms retention interval, a single probe disc was presented for 500 ms in one of the six possible positions on the imaginary circle. Participants indicated whether or not the probe disc matched one of the target discs in colour and location by button press (right

index finger for same, right middle finger for different). Randomly within each run, 50% of trials were 'same' and 50% were 'different'. Of the non-matching trials, 50% constituted a change of location, and 50% a change of colour. There were no trials in which both location and colour changed, and changes were always to a location or colour that was not present in the stimulus display. A feedback display consisting of 5 symbols arranged in a cross pattern at fixation was presented for 500 ms following each response (+ for correct, - for incorrect, and | for no response). Total trial duration was 4200 ms. Trials were presented in 3 runs of 34 trials each. The first and last trials of each run were discarded, leaving 8 trials at each set size per run. Intertrial intervals (ITI) were between 0 and 4 TR in duration and were randomized within an exponential distribution: in 50% of trials, there was no ITI after the 1500 ms response period, in 25% of trials there was a 1 TR (2200 ms) ITI, in 12.5% of trials there was a 2 TR (4400 ms) ITI, in 6.25% of trials there was a 3 TR (6600 ms) ITI, and in 3.125% of trials there was a 4 TR (8800ms) ITI. Each run was counterbalanced for load.

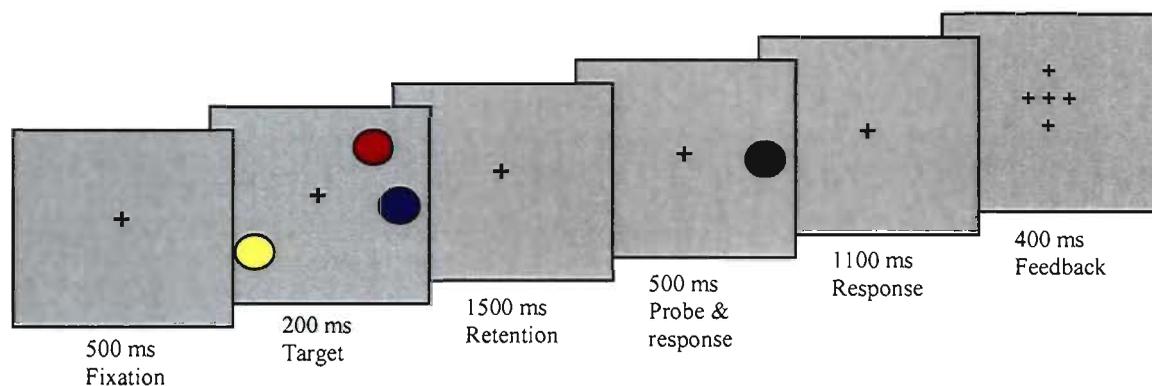


Figure 1. Task 1 – Localizer task structure. Target display contained 1, 2, 3, or 5 coloured discs.

The second task used a block design to manipulate selectively the amount of 'What' information versus the amount of 'Where' information while keeping all other stimulus factors constant. In each trial (Figure 2), a fixation cross was presented for 500ms, followed by a rapid series of 3 coloured discs at one or three of six possible locations on an imaginary circle around fixation. Each disc was presented for 200 ms with 100 ms between discs. After a 1500 ms retention interval a single probe disc was presented for 500 ms at one of the six positions on the imaginary circle. Participants indicated whether or not the probe disc matched one of the target discs in colour and location by button press (right index finger for same, right middle finger for different). Randomly within each block, 50% of trials were 'same' and 50% were 'different'. Of the non-matching trials, 50% constituted a change of location, and 50% a change of colour. There were no trials in which both location and colour changed, and changes were always to a location or colour that was not present in the stimulus display. Feedback was presented at the end of each trial using the same procedure as in the localizer task. Total trial duration was 5000 ms. Trials belonged to one of four conditions. In the What1Where1 condition, the three target discs were in the same colour and were presented at the same location. In the What3Where1 condition, the targets were in different colours but were presented at a single location. In the What1Where3 condition, three discs in the same colour were presented in three different locations. In the What3Where3 condition, three different coloured targets were presented in three different locations. Trials were presented in 4 runs, each composed of 8 blocks of 12 trials. There was a rest period of 7 TR (15.4 sec.) between blocks. Trials

were blocked by condition, with each condition occurring twice within each run, and block order counterbalanced across all 4 runs. Instructions were the same for all conditions, and were presented once at the beginning of the first run. Participants were instructed to respond ‘same’ if the colour and position of the probe disc were the same as one of the target discs, and to respond ‘different’ if either the colour or location had changed.

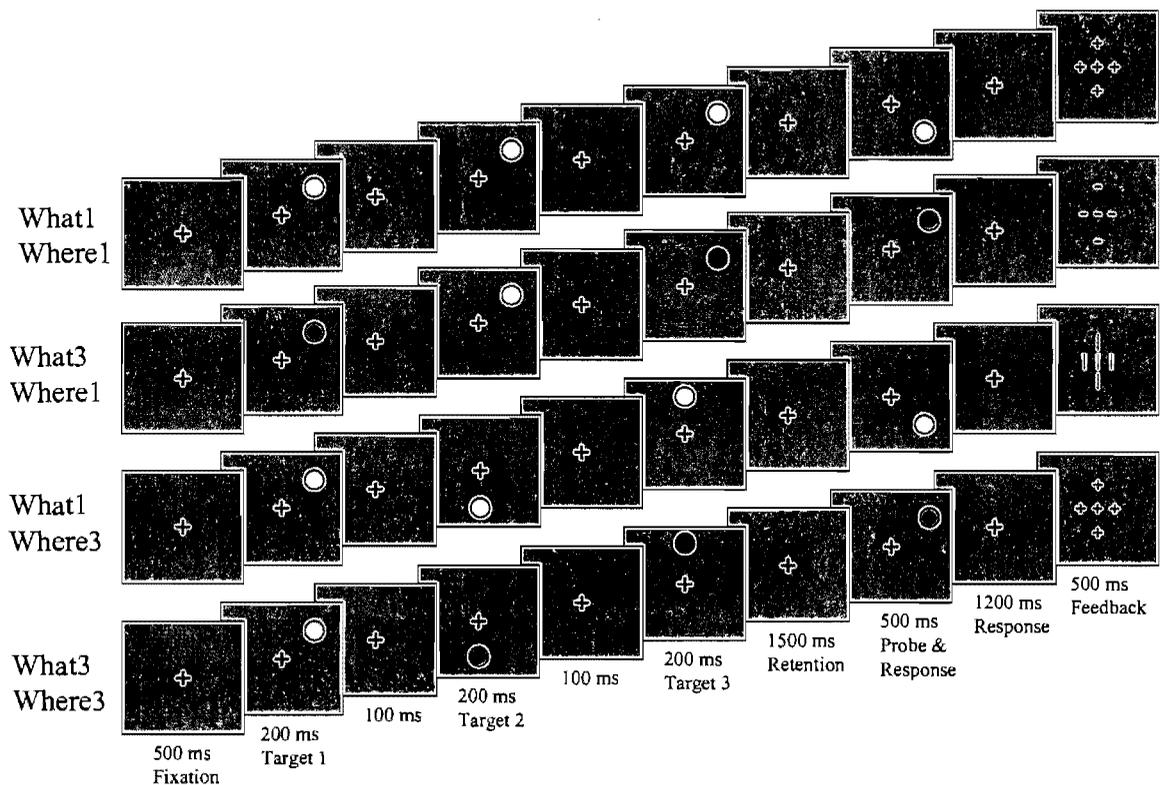


Figure 2. Task 2 – What-Where conditions and trial structure.

fMRI Methods

Low-resolution and 3-dimensional high-resolution T1-weighted anatomical images were acquired on a 3T Siemens Trio MRI system. 3D images were acquired in

28 1.2 mm-thick (1 mm × 1mm in-plane, 0 mm gap) sagittal slices. Functional T2*-weighted echoplanar images were acquired in 28 interleaved axial slices (5 mm thick, 3.75 mm × 3.75 mm in-plane, 0 mm gap, repetition time (TR) = 2200 ms, echo time (TE) = 30 ms, field of view (FOV) = 240 mm, matrix = 64 × 64) aligned parallel to the AC-PC plane. Trial presentation was synchronized to TR onset by scanner trigger pulses. Stimuli were presented on a PC running E-Prime software (Psychology Software Tools) and were back-projected onto a screen viewed by the subject through a mirror attached to the MRI head coil. fMRI parameters were identical for both the event-related and blocked-design tasks

Data Analysis

Behavioural analysis. The estimated number of items stored in VSTM for a given set size was calculated for each subject using Cowan's K formula (Pashler, 1988; Cowan, 2001):

$$K = N (\text{hit rate} + \text{correct rejection rate} - 1)$$

where K is the estimated number of items stored in VSTM and N is the number of items in the stimulus array. Accuracy rates and reaction times were also collected and repeated measures ANOVAs were conducted on the behavioural data.

fMRI analysis. fMRI data analysis was performed using Brain Voyager QX 1.9 (Brain Innovation, Maastricht, Netherlands). All functional data sets were subjected to intra-session image realignment, 3D motion correction using trilinear interpolation, correction for slice scan acquisition time using sinc interpolation, linear trend removal,

and spatial smoothing with a Gaussian filter of 8.0 mm FWHM before being analyzed. Functional and anatomical data sets were standardized into Talairach space (Talairach and Tournoux, 1988). Three subjects were excluded from analysis due to excessive motion, one was excluded because the subject fell asleep during scanning, and two were excluded because they did not show any significant activation on the statistical parametric map (SPM) of the localizer task (see below). For each subject, multiple regression analysis was performed on the localizer (Task 1) data, with regressors for each set size weighted with the corresponding individual K value and convolved with a canonical haemodynamic response function (Todd and Marois, 2004). The resulting maps were corrected for multiple comparisons using cluster threshold estimation (CTE; Forman, Cohen, Fitzgerald, Eddy, Mintun, and Noll, 1995; Goebel, Esposito, and Formisano, 2006). The pre-correction alpha level was adjusted on an individual basis, in order to compensate for inter-subject variability in signal strength, and varied between 0.0001 and 0.01. The CTE correction was then applied for a corrected alpha of 0.05. For each subject, significant voxel clusters situated in the IPS/IOS were isolated as the volumes of interest (VOI) for analysis of the What-Where task. Average time courses for the localizer task were computed within these VOIs by extracting, in each individual, an average time course for each load, and averaging these time courses across subjects. Percent signal change was computed relative to the two volumes preceding stimulus onset. A 2 (What1, What3) \times 2 (Where1, Where3) multi-subject random effects analysis of variance (ANOVA) of the What-Where data was conducted for the individually-localized IPS/IOS VOIs. Average activation levels for each

condition in the What-Where task were computed by extracting an average block time course for each condition from each subject's IPS/IOS VOI, averaging these time courses across subjects, resulting in one average block per condition, then averaging across volumes within the block to give an average activation level for each condition. Percent signal change was computed relative to the two volumes preceding block onset.

In order to ascertain whether the IPS/IOS might be divided into sub-regions that respond uniquely to identity or location information, the What-Where ANOVA was conducted for a group average IPS/IOS VOI, and SPMs were computed within the masked IPS/IOS. The group average IPS/IOS VOI was computed across all subjects who were included in the previous analysis using set-size regressors weighted with the group average K -values.

Results

Behavioural Results

All behavioural and fMRI results below are based on the 14 subjects remaining after exclusions for the reasons outlined in the previous sections. Mean response times in the localizer task increased significantly with set size (Load 1 = 693 ms; Load 2 = 766 ms; Load 3 = 813 ms; Load 5 = 872 ms), $F(3, 39) = 34.18, p < .001$, and all pairwise comparisons between set sizes were significant, $p < .01$. The average number of objects retained in VSTM (K) also increased significantly with set size: Load 1 = 0.98, Load 2 = 1.94, Load 3 = 2.57, Load 5 = 3.29, $F(3, 39) = 64.40, p < .001$, and all pairwise comparisons between set sizes were significant, $p < .01$. The average K function was

better fit by a linear model $F(1, 13) = 128.69, p < .001$ than by a quadratic model, $F(1, 13) = 0.94, p > .35$, however, a repeated measures ANOVA of the differences between K and N at each load revealed a clear divergence from a 1-to-1 encoding of presented stimuli after set size 2 (see Figure 3). The difference between K and N was of the same magnitude at Load 1 and Load 2, $F(1, 13) = 2.938, p > 0.1$, but was larger at Load 3 than at load 2, $F(1, 13) = 10.56, p < .01$, and larger still at Load 5 than at Load 3, $F(1, 13) = 27.85, p < .001$. These results suggest that the increase in K with increasing set size was less steep across larger set sizes than across smaller ones.

Two-factor repeated-measures ANOVAs were conducted on accuracy and reaction time data from the What-Where task. The accuracy scores showed a significant main effect of What, $F(1, 13) = 38.52, p < .001$, a significant main effect of Where, $F(1, 13) = 4.50, p < .05$, as well as an interaction, $F(1, 13) = 5.96, p < .05$ (Figure 4). Reaction times showed very significant main effects of both What $F(1, 13) = 61.60, p < .001$ and Where $F(1, 13) = 37.30, p < .001$, but showed no interaction, $F(1, 13) = 0.57, p > .4$ (Figure 4).

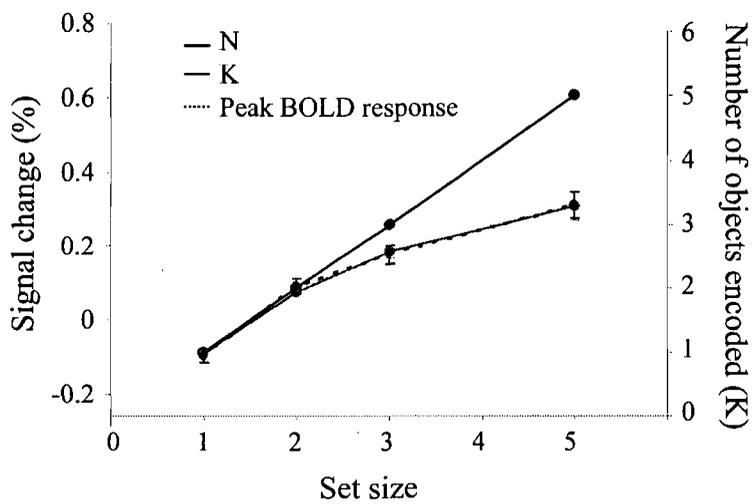


Figure 3. Average K function and peak BOLD response averaged across individual IPS/IOS VOIs plotted against 1-to-1 stimulus encoding function (N). Percent signal change is computed relative to the two volumes preceding the onset of each trial. Error bars represent standard error of the mean.

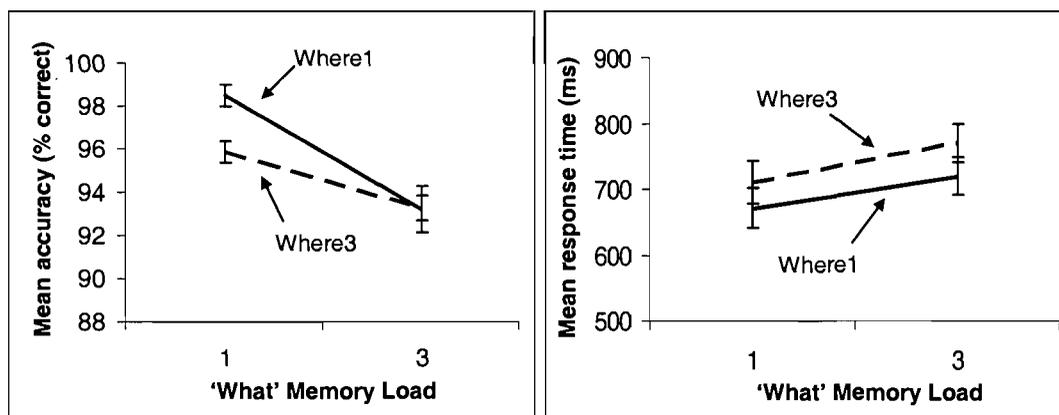


Figure 4. Accuracy and response times from the What-Where task. Accuracy scores show significant main effects of What and Where and a significant interaction. Response times show both main effects, but no interaction.

fMRI Results

The individual localizer regression identified areas of significant activation in the IPS/IOS region in all but two subjects. The average localizer time course computed across individual IPS/IOS VOIs can be seen in Figure 5. The Load 1 time course is negative because the baseline was computed from the two volumes preceding stimulus onset rather than from a control condition, and the ITI jitter was in too narrow a temporal range to always allow activation from previous trials to return to baseline. The peak BOLD response of the average time course at each load closely follows the shape of the average K function (Figure 3).

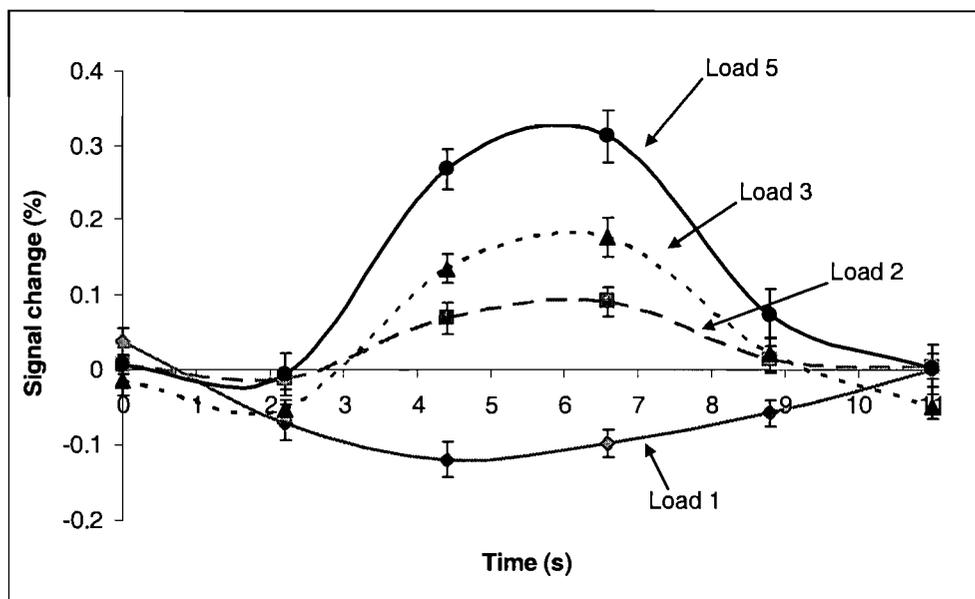


Figure 5. Average time course for the localizer task, computed across individually-localized IPS/IOS VOIs.

The multi-subject What-Where VOI ANOVA of individually localized IPS/IOS voxels, in contrast to the behavioural results, revealed no main effect of What load, $F(1,$

13) = 2.33, $p > .15$, a significant main effect of Where load, $F(1, 13) = 21.80$, $p < .001$, and no interaction, $F(1, 13) = 0.08$, $p > .77$. Post-hoc contrasts revealed that the Where effect was significant at both levels of What, $t(13) = 4.05$, $p < .001$ at What1 and $t(13) = 2.461$, $p < .02$ at What3. Average activation levels for each condition are shown in Figure 6.

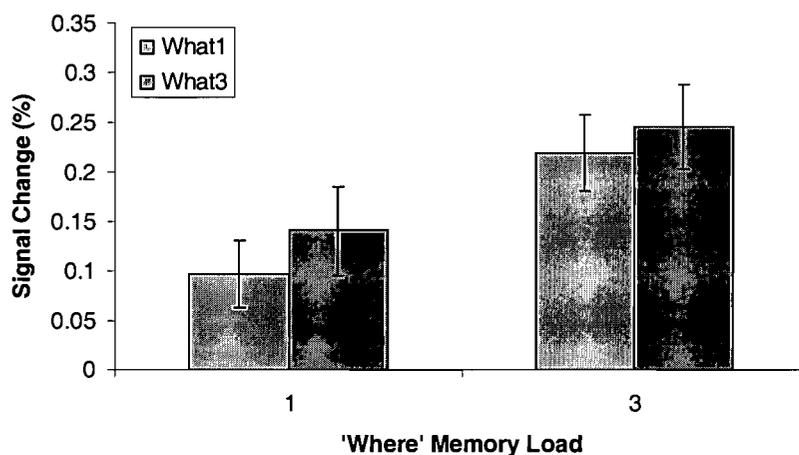


Figure 6. Average activation levels in the What-Where task. Error bars represent standard error of the mean.

The average IPS/IOS VOI computed from the localizer group data and corrected for multiple comparisons using CTE to $\alpha = .05$ is illustrated in Figure 7, panel A. The centres-of-mass were at Talairach coordinates (x, y, z) -26, -64, 35 and 25, -65, 39. SPMs (CTE-corrected to $\alpha = .05$) of the What-Where ANOVA of voxels in the average IPS/IOS mask revealed a large portion of the VOI that showed a significant main effect of Where (Figure 7, panel B), but no IPS/IOS sub-regions showed a main effect of What or an interaction. The absence of a What effect in the IPS/IOS is not due to a lack of

power, since an exploratory whole-brain analysis revealed regions of significant What-related activation elsewhere. Since the present study is concerned only with IPS/IOS activation, these other regions will not be discussed here.

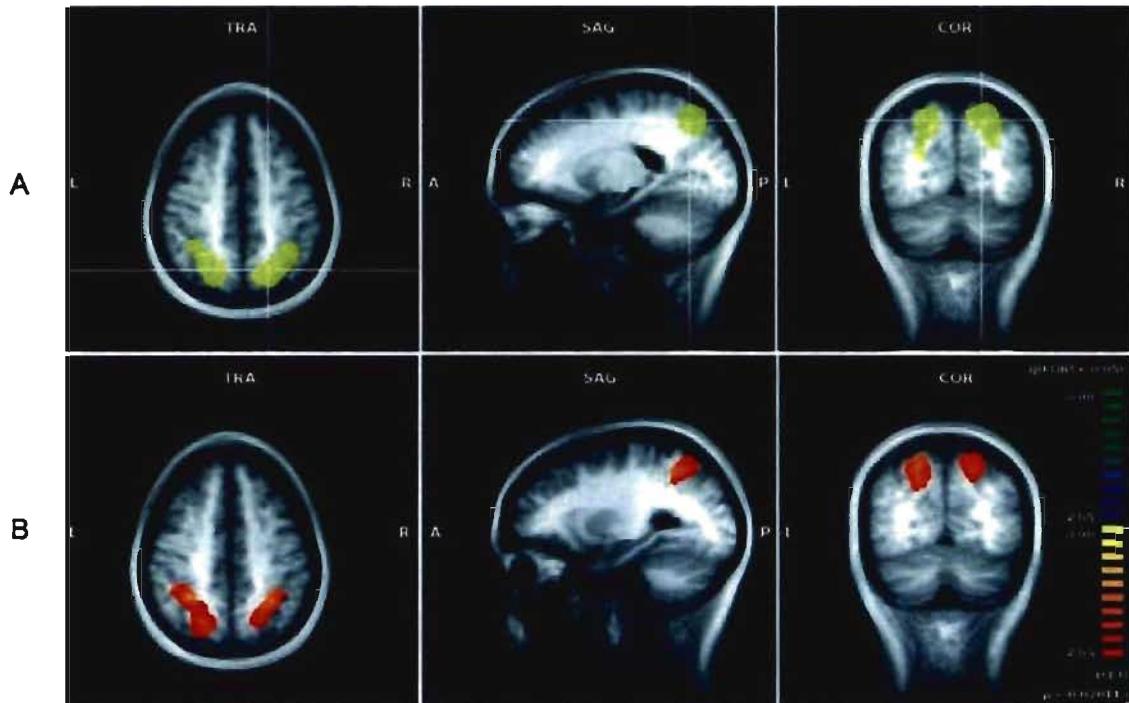


Figure 7. A) Group average IPS/IOS volume-of-interest (VOI), overlaid on an average of the 14 subjects' anatomical scans. B) Voxels showing a main effect of Where within the masked group average IPS/IOS region.

Discussion

The present study was designed to examine differences in IPS/IOS BOLD activation in response to manipulations of object identity and location information load in VSTM. This was accomplished by varying memory load independently for 'What' and 'Where' aspects of the memorized objects, without altering any other stimulus

attributes. The IPS/IOS was localized in each subject in order to examine BOLD responses specifically related to the What-Where manipulation in voxels whose activation correlated with individual VSTM capacity. Behavioural results showed effects of both What and Where loads, whereas results of the random-effects, multi-subject VOI analysis showed significant change in IPS/IOS BOLD activation only in response to manipulation of the amount of location information (Where). This suggests that while both object identity and location information influence VSTM capacity, the related activation in the IPS/IOS is primarily driven by the amount of spatial information retained in VSTM. An attempt to identify sub-regions of the IPS/IOS that respond selectively to What or Where information revealed a large sub-region that responded only to location information, but no significant sub-regions that responded only to identity information, or to the interaction of What and Where, supporting the notion that IPS/IOS activation mainly reflects the representation of spatial information. The implication for the Todd and Marois (2004; 2005) finding is that it may have been spatial information, or the requirement to conjoin spatial and color identity information (Shafritz, Gore, and Marois, 2002) that primarily drove subjects' parietal activation when they were asked to remember both the location and color identity of objects in the visual scene.

Our finding conflicts with the conclusions of Xu and Chun (2006), who posited that the IPS is functionally dissociable into superior and inferior sub-regions, with the inferior IPS indexing only spatial locations and the superior IPS indexing both location and object identity in VSTM. We observed no such dissociation, and no effect of object

identity information on IPS/IOS activation. There are, however, several methodological considerations that make it difficult to compare the present results with those of Xu and Chun. Firstly, different stimuli were used in the present study than in the Xu and Chun study. We used coloured discs as stimuli in all conditions, whereas Xu and Chun used black shapes of varying complexities. These types of stimuli likely place different demands on object VSTM. Secondly, different localization procedures were used. Xu and Chun identified their superior IPS region using a procedure very similar to the localizer used in the present study and in Todd and Marois' experiments (2004; 2005). In contrast, the inferior IPS was identified as voxels that responded more strongly to objects than to noise images, making the functional role of this region for VSTM less compelling than for voxels identified for their relationship with VSTM capacity. The VOIs identified by Todd and Marois as well as those of the present study encompassed both the superior and inferior IPS regions identified by Xu and Chun (2006). Xu and Chun also state that when superior IPS activation was "extensive", they limited this VOI to 20 voxels around the centre-of-gravity coordinates given by Todd and Marois. This statement implies that there may have been a large overlap between superior and inferior IPS VOIs had this restriction not been applied, making the justification for separating inferior and superior IPS unclear. Thirdly, in their examination of whether IPS activation tracked identity or location information, three presentation conditions were used: sequential centred (at fixation), sequential off-centre, and simultaneous off-centre. None of these conditions can be directly compared to test for differences between same and different locations – the sequential centred and sequential off-centre conditions

confound location with stimulus eccentricity, the sequential centred and simultaneous off-centre conditions again differ in stimulus eccentricity, but also in presentation rate (simultaneous or one at a time), and the sequential and simultaneous off-centre conditions can only inform us of differences related to presentation rate. In order to compensate for differences in stimulus eccentricity, Xu and Chun further subdivided the inferior IPS into regions that responded more to off-centre objects than to a noise screen, and responded more to a centred object than a square of noise presented at fixation. However, it is not clear that this procedure overcomes the eccentricity confound in the What-Where comparisons. Lastly, although stimuli were presented at different locations at encoding, it is not clear that this information was encoded and retained because all memory probes were presented at fixation. For all of these reasons, it is difficult to draw firm conclusions concerning the representation of What versus Where information in VSTM on the basis of the Xu and Chun (2006) study.

It must again be acknowledged that the present study examined colour as the object identity variable, whereas several other studies have examined VSTM for more complex stimuli (e.g., Courtney et al., 1996 (faces); Munk et al., 2002 (natural objects); Sala et al., 2003 (houses and faces); Xu and Chun, 2006 (shapes); Sala and Courtney, 2007 (abstract images)). It is possible that more complex identity variables would place a greater load than colour on object VSTM and perhaps reveal regions of capacity-related activation that respond to manipulations object complexity and that cannot be seen in the present case or in Todd and Marois's (2004; 2005) case. This would be consistent with a non-significant trend for VSTM load effects for color observed in the

present study (see Fig. 6). We hypothesize that the parietal cortex is primarily indexing the number of locations, and that capacity limitations for object identity information may be represented elsewhere, perhaps in a more ventral region. It was not possible to localize regions associated with VSTM capacity for identity information with data from the present study. Since colour was the only identity variable and the maximum number of objects was 3, there may not have been sufficient load on object VSTM to isolate regions that showed capacity-related activation profiles (in the What-Where portion of the design).

The short retention interval used in the present study did not allow us to separate activation related to encoding, retention, and retrieval phases of the memory task, due to the sluggish nature of the haemodynamic response. Nonetheless, the absence of a load-related response in the IPS for the amount of What information suggests that none of these processes (encoding, retention, retrieval) engages IPS to a greater extent when there are more objects to be processed. In contrast, clear effects of memory load were observed for Where information. Previous work in which What and Where information covaried (Todd and Marois, 2004) has shown that IPS participates in the retention of information in VSTM by measuring the BOLD response in a slow event-related design and a long retention interval. Thus, we conclude that the IPS participates mainly in the retention of information about the spatial location of objects held in VSTM.

Conclusion. Overall, the results indicate that the capacity-related activation that is observed in the IPS/IOS is mainly driven by the representation of information about the spatial location of encoded objects in VSTM.

General Discussion

The study presented above was designed to address the question of whether IPS/IOS activation previously observed in relation to VSTM capacity reflected the representation of object identity, location, or both. The experiment addressed previous methodological concerns by selectively manipulating What and Where information load without confounding it with other stimulus dimensions and without relying on participants' uncertain ability to filter out the irrelevant dimension. IPS/IOS activation, on both individual and group levels, was consistent with the regions activated in Todd and Marois (2004). Our parametric manipulation of What versus Where clarified previous findings by revealing that IPS/IOS activation primarily reflects VSTM for object location.

The findings of the present study are part of a large body of evidence from many research domains that has shown that the parietal cortex is involved in spatial processing. Studies of spatial working memory, including various neuroimaging methodologies such as fMRI (e.g., Curtis, 2006; Mohr et al., 2006; Munk et al., 2002; Postle & D'Esposito, 1999) and positron emission tomography (PET, e.g., Courtney et al., 1996; Smith & Jonides, 1998) consistently identify the parietal cortex as a key node in the cortical network supporting spatial working memory. The parietal cortex has also been shown to be implicated in other types of spatial processing such as mental rotation (Harris, Egan, Sonkkila, Tochon-Danguy, Paxinos, & Watson, 2000) and spatial attention (Shafritz et al., 2002). Neuropsychological studies have shown that spatial processing is affected when parietal function is disrupted. For example, the

phenomenon of unilateral neglect, or hemineglect, where a patient ignores and is frequently unaware of objects in space contralateral to the lesion, can occur after a lesion of the parietal lobe, usually from a stroke (Vallar & Perani, 1986). Repetitive transcranial magnetic stimulation (rTMS) has also provided insight into the effects of disrupted parietal function on spatial processing. In a spatial delayed match-to-sample task, Koch et al. (2005) found that reaction times increased when parietal function was disrupted with rTMS during the retention interval. This result is not only further evidence of parietal involvement in spatial representation, but supports the current finding that parietal activation during a VSTM task is related to the maintenance of spatial information.

The importance of the parietal cortex in spatial processing has been well-established. Its specific role in VSTM however, was less clear. The present study has shown that, in keeping with the spatial nature of the parietal cortex, capacity-related activation in the IPS reflects the maintenance of object location information in VSTM.

Bibliography

Baddeley, A. (1992a). Working memory. *Science*, 255, 556-559.

Baddeley, A. (1992b). Working memory: The interface between memory and cognition. *Journal of Cognitive Neuroscience*, 4, 281-288.

Baddeley, A., & Hitch, G. (1974). Working memory. In G.H. Bower (Ed.), *The psychology of learning and motivation* (Vol. VIII, pp. 47-90). New York: Academic press.

Courtney, S.M., Ungerleider, L.G., Keil, K., Haxby, J. 1996. Object and spatial visual working memory activate separate neural systems in human cortex. *Cerebral Cortex*. 6: 39-49.

Courtney, S.M., Ungerleider, L.G., Keil, K., Haxby, J.V. 1997. Transient and sustained activity in a distributed neural system for human working memory. *Nature*. 386: 608-611.

Cowan, N. 2001. The magical number 4 in short-term memory: A reconsideration of mental storage capacity. *The Behavioral and Brain Sciences*. 24: 87-114.

- Curtis, C.E. 2006. Prefrontal and parietal contributions to spatial working memory. *Neuroscience*. 139: 173-180.
- D'Esposito, M., Aguirre, G.K., Zarahn, E., Ballard, D., Shin, R.K., Lease, J. 1998. Functional MRI studies of spatial and nonspatial working memory. *Cognitive Brain Research*. 7: 1-13.
- Forman, S.D., Cohen, J.D., Fitzgerald, M., Eddy, W.F., Mintun, M.A., Noll, D.C. 1995. Improved assessment of significant activation in functional magnetic resonance imaging : Use of a cluster-size threshold. *Magnetic Resonance in Medicine*. 33: 636-647.
- Goebel, R., Esposito, F., Formisano, E. 2006. Analysis of functional image analysis contest (FIAC) data with Brain Voyager QX: From single-subject to cortically aligned group general lineal model analysis and self-organizing group independent component analysis. *Human Brain Mapping*. 27: 392-401.
- Harris, I., Egan, G., Sonkkila, C., Tochon-Danguy, H., Paxinos, G., Watson, J. 2000. Selective right parietal lobe activation during mental rotation: A parametric PET study. *Brain*. 123: 65-73.

- Hartley, A., & Speer, N. 2000. Locating and fractionating working memory using functional neuroimaging: Storage, maintenance, and executive functions. *Microscopy Research and Technique*. 51: 45-53.
- Haxby, J.V., Petit, L., Ungerleider, L.G., Courtney, S.M. 2000. Distinguishing the functional roles of multiple regions in distributed neural systems for visual working memory. *NeuroImage*. 11: 380–391.
- Klauer, K.C., Zhao, Z. 2004. Double dissociations in visual and spatial short-term memory. *Journal of Experimental Psychology: General*. 133: 355–381.
- Koch, G., Oliveri, M., Torriero, S., Carlesimo, G., Turriziani, P., Caltagirone, C. 2005. rTMS evidence of different delay and decision processes in a fronto-parietal neuronal network activated during spatial working memory. *Neuropsychologia*. 24: 34-39.
- Lee, D., Chun, M. 2001. What are the units of visual short-term memory, objects or spatial locations? *Perception and Psychophysics*. 63: 253–257.
- Linden, D.E.J., Bittner, R.A., Muckli, L., Waltz, J.A., Kriegeskorte, N., Goebel, R., et al. 2003. Cortical capacity constraints for visual working memory: Dissociation of fMRI load effect in a fronto-parietal network. *NeuroImage*. 20: 1518–1530.

- Luck, S.J., Vogel, E.K. 1997. The capacity of visual working memory for features and conjunctions. *Nature*. 390: 279–281.
- Mohr, H.M., Goebel, R., Linden, D.E.J. 2006. Content- and task-specific dissociations of frontal activity during maintenance and manipulation on visual working memory. *Journal of Neuroscience*. 26: 4465–4471.
- Munk, M.H.J., Linden, D.E.J., Muckli, L., Lanfermann, H., Zanella, F.E., Singer, W., et al. 2002. Distributed cortical systems in visual short-term memory revealed by event-related functional magnetic resonance imaging. *Cerebral Cortex*. 12: 866–876.
- Pashler, H. 1988. Familiarity and visual change detection. *Perception and Psychophysics*. 44: 369–378.
- Pessoa, L., Gutierrez, E., Bandettini, P.A., Ungerleider, L.G. 2002. Neural correlates of visual working memory: fMRI amplitude predicts task performance. *Neuron*. 35: 975–987.
- Postle, B.R., D'Esposito, M. 1999. “What”-then-“where” in visual working memory: An event-related fMRI study. *Journal of Cognitive Neuroscience*. 11: 585–597.

- Postle, B.R., Stern, C.E., Rosen, B.R., Corkin, S. 2000. An fMRI investigation of cortical contributions to spatial and nonspatial visual working memory. *NeuroImage*. 11: 409–423.
- Sala, J.B., Courtney, S.M. 2007. Binding of what and where during working memory maintenance. *Cortex*. 43: 5–21.
- Sala, J.B., Rämä, P., Courtney, S.M. 2003. Functional topography of a distributed neural system for spatial and nonspatial information maintenance in working memory. *Neuropsychologia*. 41: 341–356.
- Shafritz, K.M., Gore, J.C., Marois, R.M. 2002. The role of the parietal cortex in visual feature binding. *Proceedings of the National Academy of Sciences*. 99: 10917-10922.
- Smith, E., & Jonides, J. (1998). Neuroimaging analyses of human working memory. *Proceedings of the National Academy of Sciences*. 95: 12061-12068.
- Smith, E., & Jonides, J. (1999). Storage and executive processes in the frontal lobes. *Science*. 283: 1657-1661.

- Stevanovski, B., Jolicœur, P. 2007. Visual short-term memory: Central capacity limitations in short-term consolidation. *Visual Cognition*. 15: 532–563.
- Talairach, J., Tournoux., P. 1988. Co-planar stereotaxic atlas of the human brain. New York: Thieme.
- Todd, J.J., Marois, R. 2004. Capacity limit of visual short-term memory in human posterior parietal cortex. *Nature*. 428: 751–754.
- Todd, J.J., Marois, R. 2005. Posterior parietal cortex activity predicts individual differences in visual short-term memory capacity. *Cognitive, Affective, and Behavioral Neuroscience*. 5: 144–155.
- Vallar, G., Perani, D. 1986. The anatomy of unilateral neglect after right-hemisphere stroke lesions: A clinical/CT-correlation study in man. *Neuropsychologia*. 24: 609-622.
- Vogel, E.K., Machizawa, M. 2004. Neural activity predicts individual differences in visual working memory capacity. *Nature*. 428: 748–751.

- Vogel, E.K., Woodman, G.F., Luck, S.J. 2001. Storage of features, conjunctions, and objects in visual working memory. *Journal of Experimental Psychology: Human Perception and Performance*. 27: 92–114.
- Vuontela, V., Rämä, P., Raninen, A., Aronen, H.J., Carlson, S. 1999. Selective interference reveals dissociation between memory for location and colour. *NeuroReport*. 10: 2235–2240.
- Wang, P., & Bellugi, U. (1994). Evidence from two genetic syndromes for a dissociation between verbal and visual-spatial short-term memory. *Journal of Clinical & Experimental Neuropsychology*. 16: 317-322.
- Xu, Y., Chun, M.M. 2006. Dissociable neural mechanisms supporting visual short-term memory for objects. *Nature*. 440: 91–95.