

“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 intraparietal sulcus (IPS) has been closely linked to limitations of visual short-term memory capacity (VSTM; Todd and Marois 2004; Xu and Chun 2006). It is not clearly known, however, to what extent IPS activation reflects VSTM for object identity (What) versus spatial location (Where) information. The present study was designed to manipulate selectively the amount of What and Where information retained in VSTM in order to determine, using functional magnetic resonance imaging, the effect of VSTM for each of these 2 dimensions on IPS activation. The results showed an increase in IPS activation only in response to increasing Where memory load, with no effect of What load suggesting that capacity-related activation in the IPS primarily reflects the amount of spatial information retained in VSTM.

Keywords: cognition, functional neuroimaging, parietal cortex, visual memory capacity, visual working memory

Introduction

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 et al. 2001). Investigations of the neural substrates of VSTM have revealed a large functional network in the lateral prefrontal and parietal cortices (Courtney et al. 1997; D’Esposito et al. 1998; Postle and D’Esposito 1999; Haxby et al. 2000; Postle et al. 2000; Munk et al. 2002; Pessoa et al. 2002; Linden et al. 2003; Sala et al. 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 behavioral 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 blood oxygen level-dependent (BOLD) functional magnetic resonance imaging (fMRI) signal in the intraparietal and intraoccipital sulci (IPS/IOS) increased up to set size 3 or 4 but leveled 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.

The findings of Todd and Marois (2004, 2005) are consistent with electrophysiological studies that observe a lateralized event-related potential (ERP) response over posterior parietooccipital sites that is strongly modulated by the number of visual objects retained in memory and that reaches asymptote at each subject’s individual VSTM capacity (Vogel and Machizawa 2004; Jolicoeur et al. 2008; Luria et al. 2009). Magnetoencephalography shows that one important source for this ERP is in the parietal cortex, in or near the intraparietal sulcus (IPS) (Robitaille et al. 2009; see also Grimault et al. 2009). A question that remains unanswered, however, is what kind of information is indexed by the capacity-related activation in the IPS/IOS. In the experiments of Todd and Marois, subjects retained both the identity (color) and location of objects in the memory array. Behavioral evidence suggests that VSTM stores for object identity and location are dissociable (Vuontela et al. 1999; Lee and Chun 2001; Klauer and Zhao 2004), and several neuroimaging studies have observed a dorsal-ventral dissociation between spatial and object working memory processing streams (Courtney et al. 1996; Munk et al. 2002; Sala et al. 2003; Mohr et al. 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 subregions 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 1 of the 2 stimulus dimensions (Todd and Marois 2004), which have been shown to attenuate dissociations between domain-specific activations (Postle et al. 2000), or confounded location information with stimulus presentation parameters such as eccentricity and presentation rate (Xu and Chun 2006), leading to alternative 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.

We devised 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., colored disks) convey information about both What (i.e., color) 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 even when only one of these features is probed on any given trial. This strategy may be particularly adaptive in event-related designs in which the task-relevant information can vary from trial to trial. To circumvent these

limitations, our approach was to present 3 colored disks sequentially and to vary the number of colors in the sequence, the number of locations, or both. By presenting these various alternatives in separate blocks of trials, subjects were more likely to use a strategy in which they encoded only the distinct colors, distinct locations, or both, depending on the experimental condition in that block of trials. In our experimental design, there were 4 blocked conditions—What1-Where1, What3-Where1, What1-Where3, and What3-Where3—which represented the orthogonal manipulation of memory load for What (1 vs. 3) and memory load for Where (1 vs. 3) (Fig. 1). Consider first the What3-Where1 condition, in which 3 disks of different colors (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 3 distinct colors 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 disk). Relative to the What3-Where1, the What1-Where1 condition required only encoding a single color while providing a control for the amount of information about Where (always one in these blocks). If IPS/IOS stores information about spatial location, but not color, then the activation in this region should be comparable in these 2 conditions. If, in contrast, IPS/IOS stores information about object identity (color, 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 color constant, relative to the What1-Where1 condition. The What3-Where3 condition represented the high load condition in both dimensions, provided additional anchor points for pairwise comparisons, and enabled us to assess interactions in the full 2 × 2 design.

Thus, our experimental design employed stimuli designed to vary memory load independently in terms of What information (by varying the number of distinct colors to remember) and Where information (by varying the number of different spatial locations to remember). Furthermore, the blocked presenta-

tion of the various memory-load conditions was designed to emphasize to subjects that the number of colors 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), we anticipated that subjects would minimize the processing required to succeed in the task by anticipating the same number of colors and locations in all trials within a block. Finally, a critical aspect of the stimuli was that the number of presented disks was the same in all conditions, and the retinal eccentricity of the stimuli was 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 color 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 Québec at Université de Montréal.

Study Design

The study was composed of 2 separate tasks. The first task used a fast event-related design to localize the IPS/IOS and was modeled after the delayed match-to-sample task used by Todd and Marois (2004). In each trial (Fig. 2), a fixation cross was presented for 500 ms followed by an array of 1, 2, 3, or 5 colored disks, each in a different color (red, blue, green, orange, yellow, or pink). The disks were presented at 6 possible locations on an invisible circle around fixation for 200 ms. After a 1500-ms retention interval, a single probe disk was presented for 500 ms in 1 of the 6 possible positions on the imaginary circle. Participants indicated whether the probe disk matched one of the target disks in color and location by button press (right index finger for same, right middle finger for different). Randomly within each run, 50% of trials

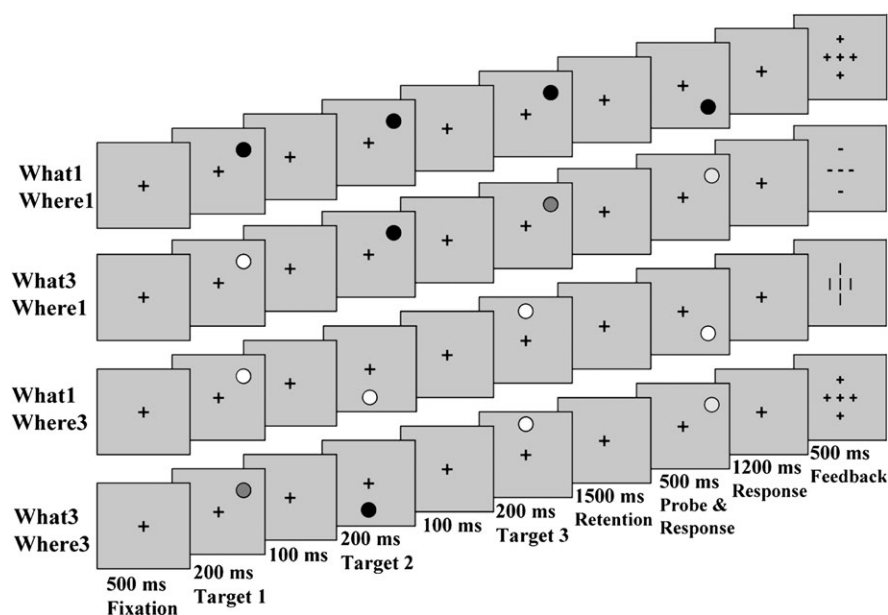


Figure 1. Task 2—What-Where conditions and trial structure. Different shades of grayscale represent different colors, with the exception of the background.

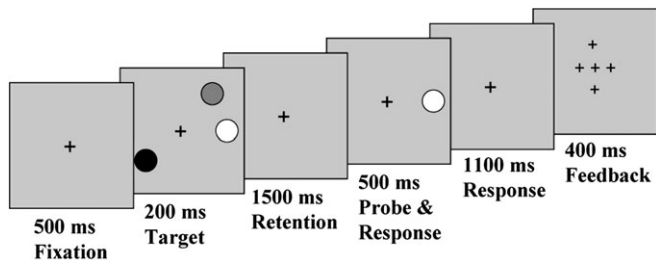


Figure 2. Task 1—localizer task structure. Target display contained 1, 2, 3, or 5 colored disks.

were “same” and 50% were “different.” Of the nonmatching trials, 50% constituted a change of location and 50% a change of color. There were no trials in which both location and color changed, and changes were always to a location or color 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 repetition times (TRs) in duration and were randomized with exponentially distributed proportions: 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 (8800 ms) ITI. Each run was counterbalanced for load.

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 (Fig. 1), a fixation cross was presented for 500 ms, followed by a rapid series of 3 colored disks at 1 or 3 of 6 possible locations on an imaginary circle around fixation. Each disk was presented for 200 ms with 100 ms between disks. After a 1500-ms retention interval, a single probe disk was presented for 500 ms at 1 of the 6 positions on the imaginary circle. Participants indicated whether the probe disk matched one of the target disks in color 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 nonmatching trials, 50% constituted a change of location and 50% a change of color. There were no trials in which both location and color changed, and changes were always to a location or color 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 1 of 4 conditions. In the What1-Where1 condition, the 3 target disks were in the same color and were presented at the same location. In the What3-Where1 condition, the targets were in different colors but were presented at a single location. In the What1-Where3 condition, 3 disks in the same color were presented at 3 different locations. In the What3-Where3 condition, 3 different colored targets were presented in 3 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 s) between blocks. Trials were blocked by condition, with each condition occurring twice within each run, and block order counterbalanced across the 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, as quickly and accurately as possible, “same” if the color and position of the probe disk were the same as one of the target disks and to respond “different” if either the color or location had changed.

fMRI Methods

Low-resolution and 3D high-resolution T1-weighted anatomical images were acquired on a 3T Siemens Trio scanner’s system. Three-dimensional images were acquired in 28 sagittal slices of 1.2-mm thickness (1 × 1 mm in-plane, 0-mm gap). Functional T2*-weighted echoplanar images were acquired in 28 interleaved axial slices (5 mm thick, 3.75 × 3.75 mm

in-plane, 0-mm gap, TR = 2200 ms, echo time = 30 ms, field of view = 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 scanner’s head coil. Scanner parameters were identical for both the event-related and blocked-design tasks.

Data Analysis

Behavioral 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), $K = N$ (hit rate + 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 analyses of variance (ANOVAs) were conducted on the behavioral data.

fMRI Analysis

fMRI data analysis was performed using BrainVoyager QX 1.9 (Brain Innovation, Maastricht, the Netherlands). All functional data sets were subjected to intrasession 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 full-width half-maximum 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, 1 was excluded because the subject fell asleep during scanning, and 2 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 hemodynamic response function (Todd and Marois 2004). The resulting maps were corrected for multiple comparisons using cluster threshold estimation (CTE; Forman et al. 1995; Goebel et al. 2006). The precorrection alpha level was adjusted on an individual basis, in order to compensate for intersubject 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 (VOIs) for analysis of the What-Where task (Task 2). 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 2 volumes preceding stimulus onset.

A 2 (What1, What3) × 2 (Where1, Where3) multisubject random-effects 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 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 2 volumes preceding block onset.

In order to verify that any lack of effect in the VOI analyses would not be due to a lack of power, a whole-brain random-effects ANOVA was also conducted on the group data, and resulting SPMs corrected to $\alpha = 0.05$. If regions of activation emerged from this analysis, it could not be said that the more powerful (due to the greatly reduced number of voxelwise comparisons) VOI analysis was simply not sensitive enough to detect an effect.

Finally, in order to examine whether the IPS/IOS VOI defined in the localizer task might contain subregions that respond uniquely to identity or location information, an SPM of the What-Where ANOVA was conducted for voxels contained inside the group average IPS/IOS VOI by applying a mask to the rest of the brain.

Results

Behavioral Results

All behavioral and fMRI results below are based on the 14 subjects remaining after exclusions for the reasons outlined in the previous sections. Mean response times (RTs) in the localizer task increased significantly with set size (load 1, mean = 693 ms; set size 2, mean = 766 ms; set size 3, mean = 813 ms; set size 5, mean = 872 ms), $F_{3,39} = 34.18$, $P < 0.001$, and all pairwise comparisons between set sizes were significant, $P < 0.01$. 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, $F_{3,39} = 64.40$, $P < 0.001$), and all pairwise comparisons between set sizes were significant, $P < 0.01$. The average K function was better fit by a linear model ($F_{1,13} = 128.69$, $P < 0.001$) than by a quadratic model ($F_{1,13} = 0.94$, $P > 0.35$); 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 Fig. 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 ($F_{1,13} = 10.56$, $P < 0.01$) and larger still at load 5 than at load 3 ($F_{1,13} = 27.85$, $P < 0.001$). 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 ($F_{1,13} = 38.52$, $P < 0.001$), a significant main effect of Where ($F_{1,13} = 4.50$, $P < 0.05$), as well as an interaction ($F_{1,13} = 5.96$, $P < 0.05$; Fig. 4a). Reaction times showed very significant main effects of both What ($F_{1,13} = 61.60$, $P < 0.001$) and Where ($F_{1,13} = 37.30$, $P < 0.001$) but showed no interaction ($F_{1,13} = 0.57$, $P > 0.4$; Fig. 4b).

fMRI Results

Task 1

The individual localizer regression analysis identified areas of significant activation in the IPS/IOS region in all but 2 subjects. The average localizer time course computed across individual

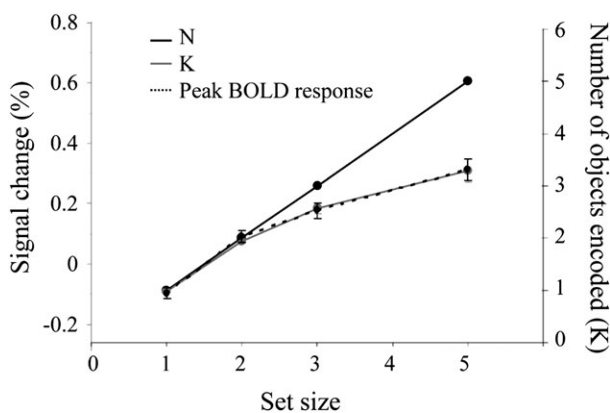


Figure 3. Average K function and peak BOLD response averaged across individual IPS/IOS VOIs plotted against 1-to-1 stimulus encoding function (N). Percent signal change is computed relative to the 2 volumes preceding the onset of each trial. Error bars represent standard error of the mean.

IPS/IOS VOIs can be seen in Figure 5. The load 1 time course is negative because the baseline was computed from the 2 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 (Fig. 3).

The average IPS/IOS VOI computed from the localizer group data and corrected for multiple comparisons using CTE to $\alpha = 0.05$ is illustrated in Figure 7, panel A. The centers of mass were at Talairach coordinates (x, y, z) -26, -64, 35, and 25, -65, 39.

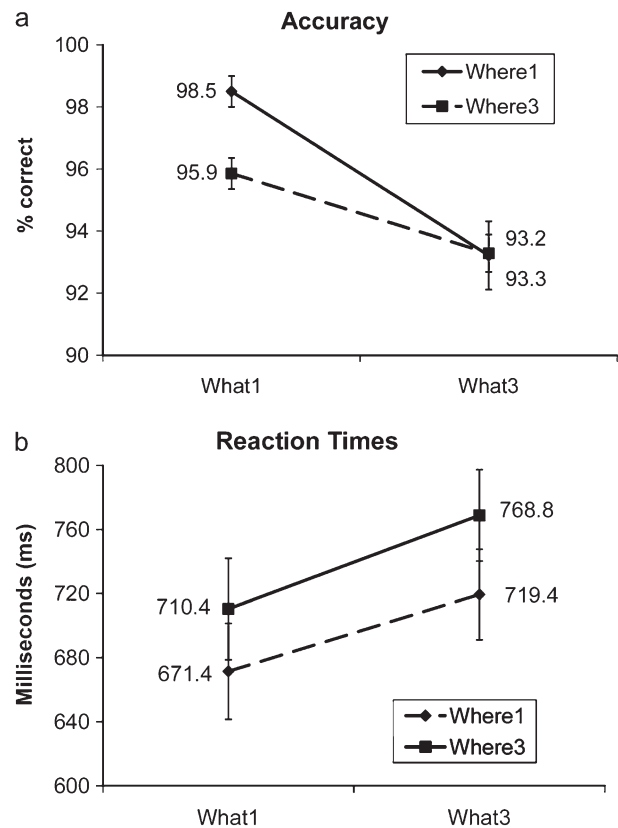


Figure 4. a) Accuracy in the What-Where task. Accuracy scores show significant main effects of What and Where and a significant interaction. (b) Reaction times in the What-Where task. Reaction times show both main effects but no interaction.

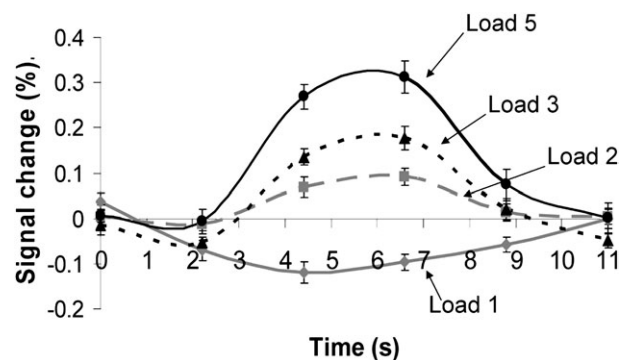


Figure 5. Average time course for the localizer task, computed across individually localized IPS/IOS VOIs.

Task 2

The multisubject What-Where ANOVA of individually localized IPS/IOS VOIs, in contrast to the behavioral results, revealed no main effect of What load ($F_{1,13} = 2.33, P > 0.15$), a significant main effect of Where load ($F_{1,13} = 21.80, P < 0.001$), and no interaction ($F_{1,13} = 0.08, P > 0.77$). Post hoc contrasts revealed that the Where effect was significant at both levels of What, $t_{13} = 4.05, P < 0.001$, at What1 and $t_{13} = 2.461, P < 0.02$, at What3. Average activation levels for each condition are shown in Figure 6. The IPS/IOS response to changes in Where load (0.1137 difference in percent signal change) was more than 3 times as large as the response to changes in What load (0.0352 difference in percent signal change), and this difference was statistically significant, $t_{13} = 2.644, P < 0.02$, showing that the IPS/IOS is more sensitive to Where load than What load.

SPMs (CTE corrected to $\alpha = 0.05$) 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

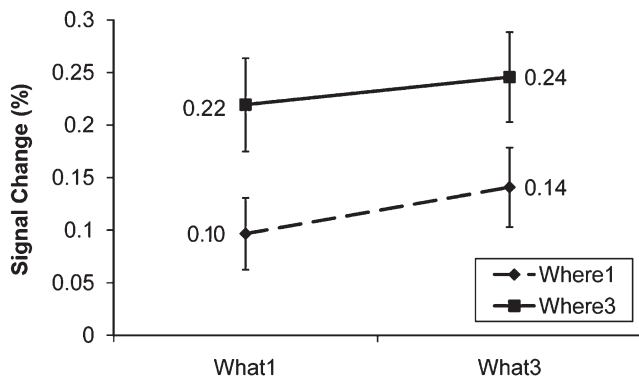


Figure 6. Average activation levels in the What-Where task. Error bars represent standard error of the mean.

Where (Fig. 7, panel B), but no IPS/IOS subregions of the VOI showed a main effect of What or an interaction.

In the exploratory analysis, whole-brain maps of the What and Where main effects and interactions were computed (Talairach coordinates of clusters of significant activation may be found in Table 1). The Where main effect was significant ($CTE \alpha \leq 0.05$) in the left and right IPS, left superior frontal sulcus near the junction with the precentral sulcus—the location of the putative human frontal eye fields (FEFs; Paus 1996)—right postcentral gyrus, and the posterior tip of the left lingual gyrus. The What main effect was significant in the left orbital gyrus, the posterior end of the left cingulate gyrus, the left precentral sulcus, and the right inferior parietal lobule. Significant interaction effects were also observed in the anterior cingulate sulcus and the precuneus, bilaterally. The results of this exploratory whole-brain analysis suggest that the absence of a What effect in the IPS/IOS in the VOI analysis is not due to a lack of power since it revealed regions of significant What-related activation in several brain regions. It is important to note that, unlike the IPS/IOS VOI isolated with the VSTM localizer task, the regions identified in the whole-brain analysis are not necessarily related to VSTM: they simply reflect voxels that showed different levels of activation at load 3 than at load 1, which could be due to any number of perceptual or task-related factors. Speculation as to the functions of the regions identified in the whole-brain analysis is beyond the scope of this study. The whole-brain analysis was simply used as a means to confirm that the absence of a What main effect in the IPS/IOS was not due to a lack of statistical power.

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

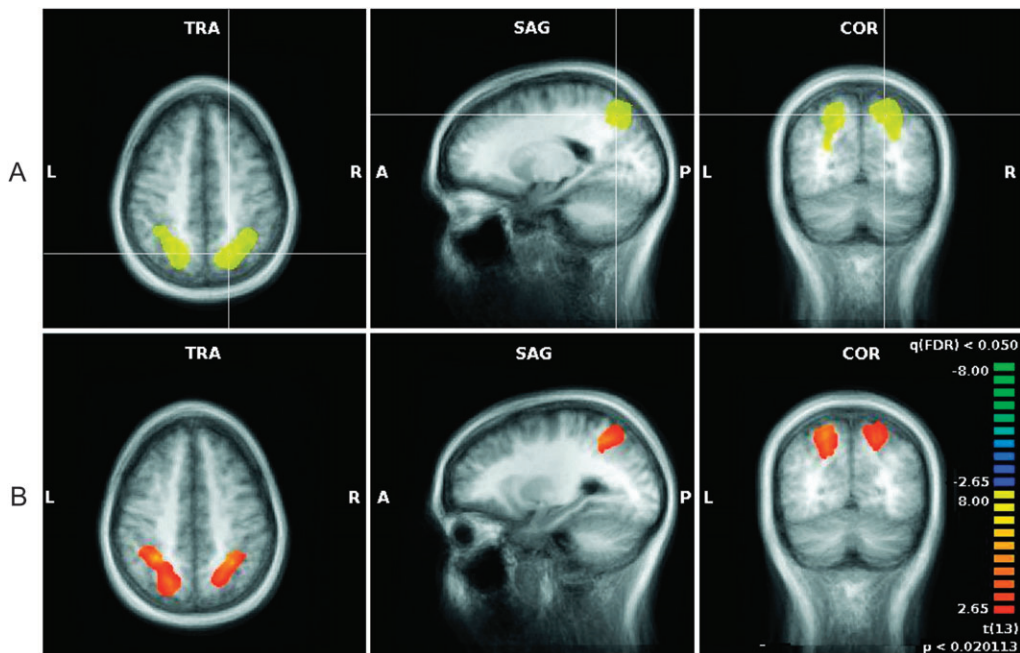


Figure 7. A) Group average IPS/IOS VOI, overlaid on an average of the 14 subjects' anatomical scans. (B) Voxels showing a main effect of Where within the masked group average IPS/IOS region.

Table 1

Talairach coordinates of significant clusters from the whole-brain What-Where ANOVA

	Mean x	Mean y	Mean z	Number of voxels
Where main effect				
Right IPS	24	-60	47	13546
Right postcentral gyrus	41	-33	58	9292
Left IPS	-27	-52	45	7297
Left lingual gyrus	-17	-96	-13	1779
Left FEF	-22	-12	62	2582
What main effect				
Right inferior parietal lobule	52	-25	27	6851
Left orbital gyrus	-3.6	31	-1.2	3695
Left posterior cingulate	-7.7	-54	26	3534
Left precentral sulcus	-38	-3	31	2162
Interaction				
Bilateral precuneus	2.8	-52	30	4778
Bilateral anterior cingulate sulcus	-0.71	38	8.6	3316

accomplished by varying memory load independently for What and Where aspects of the memorized objects, without altering any other stimulus attribute. 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. Behavioral results showed effects of both What and Where loads, whereas results of the random-effects multisubject 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.

Accuracy results (Fig. 4*a*) show main effects of both What load and Where load, as well as an interaction, such that increasing the What memory load was associated with a slight decrease in accuracy for both levels of Where load and increasing the Where load decreased accuracy when all items were of the same color (What = 1) but had minimal effects when the items were of different colors (What = 3). Accuracy results cannot be interpreted without also considering the accompanying RTs. In the RTs, we found clear effects (significant) for both factors, consistent with the expectation that increasing load increased task difficulty. Here, the effects were statistically additive. The slight and not statistically significant deviations from additivity in the RTs might reflect minor tendencies toward speed-accuracy tradeoffs. Given that the deviation from additivity in the accuracy results was small in magnitude, and that the RTs were statistically additive, we cautiously focus on the additivity of the What and Where effects found in the RT results, which we believe reflects the true state of affairs, namely that increasing the number of locations (Where) and increasing the number of colors (What) both increased memory load.

Meanwhile, an attempt to identify subregions of the IPS/IOS that respond selectively to What or Where information revealed a large subregion that responded only to location information, but no significant subregions 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, even though both What load and Where load increase memory load as measured by accuracy and reaction times. 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 et al. 2002) that primarily drove parietal activations when subjects were asked to remember both the location and color identity of objects in the visual scene.

Our findings appear to conflict with the conclusions of Xu and Chun (2006), who posited that the IPS is functionally dissociable into superior and inferior subregions, 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 significant 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 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 the experiments of Todd and Marois (2004, 2005). In contrast, their 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 specific than for voxels identified for their relationship with VSTM load and VSTM capacity. The ROIs identified by Todd and Marois as well as those of the present study included both the superior and inferior IPS regions identified by Xu and Chun. However, the inferior IPS localization procedure used by Xu and Chun may have recruited a more extensive region than was activated in the current study, and therefore, their conclusions may be based on activity in regions that are not specifically related to capacity limitations in VSTM. The inferior IPS has been shown to be instrumental for visual attention (e.g., Wojciulik and Kanwisher 1999), which in turn is instrumental for VSTM, and while it is important to consider the effects of attentional processes on VSTM, the present study focuses on regions directly related to storage in VSTM, which were not necessarily singled out by the inferior IPS localization procedure used by Xu and Chun. Secondly, there are important differences in the stimuli used across studies. We used colored disks as stimuli in all conditions, whereas Xu and Chun used black shapes of varying complexities. Colors are easier to remember than shapes (e.g., Song and Jiang 2006). This may explain why we did not observe significant effects of What load in IPS/IOS, whereas Xu and Chun observed an object identity VSTM load effect in the superior IPS. However, this comparison is complicated by the identity-versus-location manipulation of Xu and Chun. In order to assess whether IPS activation tracked identity or location information, 3 presentation conditions were used by Xu and Chun: sequential centered (at fixation), sequential off-center, and simultaneous off-center. None of these conditions can be directly compared with test for differences between same and different locations—the sequential-centered and sequential off-center conditions confound location with stimulus eccentricity, the sequential-centered and simultaneous off-center conditions again differ not only in stimulus eccentricity but also in presentation rate (simultaneous or one at a time), and the sequential and simultaneous off-center 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-center objects than to a noise screen and responded more to a centered 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. Nonetheless, Xu and Chun observed a load effect in the superior IPS in their sequential-centered condition, which would not be expected if this region indexes only location VSTM, as the present findings suggest. The possibility must be considered, therefore, that some amount of object identity information is stored by the IPS. The absence of a significant What effect in the present study, where Xu and Chun observed one, may be the result of the different localization procedures or of the use of simpler stimuli that did not put as much load on What VSTM as the shapes used in Xu and Chun. Indeed, while the present study examined color as the object identity variable, several other studies, using more complex stimuli, have also found VSTM-related activation in the IPS (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]). Thus, it is possible that more complex identity variables would place a greater load than color on object VSTM and perhaps reveal object-sensitive regions showing capacity-related activation in IPS/IOS. This would be consistent with a nonsignificant trend for VSTM load effects for color observed in the present study (see Fig. 6). In any case, our results clearly show that even if IPS/IOS has some sensitivity to What load, the sensitivity to Where load is significantly greater. Therefore, we hypothesize that the parietal cortex is primarily indexing the number of locations and that capacity limitations for object identity information may be represented more strongly elsewhere, perhaps in a more ventral region. The exploratory whole-brain analysis revealed several areas showing a main effect of What load; however, it is difficult to speculate on the role of these regions in VSTM because none of these regions appeared as capacity related in the localizer task and do not consistently appear in other studies of object VSTM. Future study should address this issue since the nonsignificant trend toward a What load effect in the IPS suggests that this region may also play a role in object identity processing or in the integration of identity and location in VSTM.

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 hemodynamic 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) engage 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, to the extent that IPS activation in VSTM tasks reflects activity required to maintain information in VSTM, the present results suggest that this activity participates mainly in the retention of information about the spatial location of objects held in VSTM.

Conclusions

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.

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