

# Discrete Capacity Limits and Neuroanatomical Correlates of Visual Short-Term Memory for Objects and Spatial Locations

Nikos Konstantinou,<sup>1,2\*</sup> Fofi Constantinidou,<sup>1,2</sup> and Ryota Kanai<sup>3,4,5,6</sup>

<sup>1</sup>Center for Applied Neuroscience, University of Cyprus, Nicosia, Cyprus

<sup>2</sup>Department of Psychology, University of Cyprus, Nicosia, Cyprus

<sup>3</sup>Sackler Centre for Consciousness Science, University of Sussex, Falmer BN1 9QJ, United Kingdom

<sup>4</sup>School of Psychology, University of Sussex, Falmer, BN1 9QH, United Kingdom

<sup>5</sup>Department of Neuroinformatics, Araya Brain Imaging, Tokyo, Japan

<sup>6</sup>YHouse Inc, New York, New York

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**Abstract:** Working memory is responsible for keeping information in mind when it is no longer in view, linking perception with higher cognitive functions. Despite such crucial role, short-term maintenance of visual information is severely limited. Research suggests that capacity limits in visual short-term memory (VSTM) are correlated with sustained activity in distinct brain areas. Here, we investigated whether variability in the structure of the brain is reflected in individual differences of behavioral capacity estimates for spatial and object VSTM. Behavioral capacity estimates were calculated separately for spatial and object information using a novel adaptive staircase procedure and were found to be unrelated, supporting domain-specific VSTM capacity limits. Voxel-based morphometry (VBM) analyses revealed dissociable neuroanatomical correlates of spatial versus object VSTM. Interindividual variability in spatial VSTM was reflected in the gray matter density of the inferior parietal lobule. In contrast, object VSTM was reflected in the gray matter density of the left insula. These dissociable findings highlight the importance of considering domain-specific estimates of VSTM capacity and point to the crucial brain regions that limit VSTM capacity for different types of visual information. *Hum Brain Mapp* 00:000–000, 2016. © 2016 Wiley Periodicals, Inc.

**Key words:** visual short-term memory; voxel-based morphometry; capacity limits

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## INTRODUCTION

Working memory is thought to be a temporary storage system for information encoded by the sensory cortex [Bergmann et al., 2016; Harrison and Tong, 2009; Serences et al., 2009]. As such, working memory provides the essential link between sensory encoding and higher cognitive functions, and thus underpins our ability for complex thought and action [Baddeley, 2007]. Despite its crucial role, the evidence suggests that the capacity of working memory is severely limited. For instance, recent estimates indicate that the maximum number of visual objects that can be maintained in visual short-term memory (VSTM) ranges between three and four items, and it is subject to

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\*Correspondence to: Nikos Konstantinou, Department of Psychology, University of Cyprus, 75 Kallipoleos, P.O. Box 20537, CY, 1678, Nicosia, Cyprus. E-mail: nkonstantinou@gmail.com

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large interindividual variability [Conway et al., 2001; Cowan et al., 2005; Luck and Vogel, 1997; Todd and Marois, 2004; Vogel and Machizawa, 2004; Vogel et al., 2005; Vogel et al., 2001].

Evidence from genetic studies indicates that the large interindividual variability of the capacity to maintain visual information in short-term memory is significantly influenced by genes [Ando et al., 2001; Luciano et al., 2001]. Genetic effects on VSTM capacity manifest themselves during development via impact on brain activity and gray matter (GM) volume [Dumontheil et al., 2011]. Taken together, such evidence indicates that interindividual variability in VSTM capacity may also be determined via genetic influences on the structure of the brain.

Indeed, a gradually accumulating body of evidence from computational neuroanatomy of high-resolution MRI brain images revealed that the structure of the brain exhibits a systematic relationship with an individual's behavior and cognitive skills [Kanai and Rees, 2011]. More relevant to working memory, [Bergmann et al. 2016] have recently shown that the structure of primary visual cortex can specifically predict performance on a VSTM task. Surprisingly, it still remains unclear whether the structure of other brain areas previously implicated in VSTM maintenance correlates with the limited capacity of VSTM. Behavioral evidence using the typical delayed match-to-sample task for estimating VSTM capacity suggests that working memory is not unitary and involves dissociable systems for the storage of visual information regarding the visual-identity and the spatial location of an object [e.g. Klauer and Zhao, 2004; Lee and Chun, 2001; Vuontela et al., 1999].

Recent neuroimaging studies supported the behavioral findings for the fractionation of VSTM into separate object and spatial components across the entire brain (we term this the *information segregation hypothesis of VSTM*) [Bellgowan et al., 2009; Buffalo et al., 2006; Cichy et al., 2011; A. Harrison et al., 2010; Mohr et al., 2006; Ranganath et al., 2004; Sala and Courtney, 2007; Sala et al., 2003]. Research on the neurophysiological underpinnings of VSTM has revealed a dorsal-ventral dissociation between object and spatial activations [Courtney et al., 1996; Mohr et al., 2006; Munk et al., 2002; Sala et al., 2003]. Early nonhuman primate studies supported the information segregation hypothesis by demonstrating that perceptual information related to an object's spatial location is processed in a dorsal visual pathway, whereas information related to the object's identity (e.g., color, shape, texture) is processed independently in a ventral visual pathway [Desimone and Ungerleider, 1986; Desimone et al., 1985; Felleman and Van Essen, 1991; Mishkin et al., 1983; Ungerleider et al., 1983; Ungerleider and Mishkin, 1982]. Neuropsychological and neuroimaging studies [e.g., Goodale and Milner, 1992; Haxby et al., 1991, 1994; James et al., 2003; Goodale and Milner, 1995; Newcombe and Russell, 1969] have also confirmed this object-spatial information segregation in the dorsal and ventral visual pathways.

However, other functional neuroimaging studies investigating visual perception of object and spatial information have challenged the information segregation hypothesis, demonstrating neural activations related to both perception of object properties and perception of an object's spatial location in both the dorsal and the ventral visual streams [Konen and Kastner, 2008; Kravitz et al., 2010; Petit et al., 1998; Sereno and Maunsell, 1998; Sereno and Lehy, 2011; Zachariou et al., 2014]. The neuroimaging literature investigating the neural correlates of VSTM maintenance of object and spatial information also produced some results contradictory to the information segregation hypothesis [Esposito et al., 1998; McCarthy et al., 1994; Owen et al., 1998; Petit et al., 1998; Postle and Esposito, 1999a, 1999b].

The aim of the present study was therefore to separately estimate the capacity for object identity and spatial location, and assess the relationship between individual variability in brain anatomy and such distinct individual estimates of object and spatial VSTM capacity. For this purpose, we utilized a pool of meaningless letter-like symbols that are not readily nameable (see [Alvarez and Cavanagh, 2004; Konstantinou et al., 2014], experiment 2b, for similar manipulations of VSTM load) and estimated VSTM capacity using an adaptive staircase up/down method which allows for the rapid estimation of VSTM capacity.

In line with the hypothesis of information segregation in the human brain, we predicted distinct individual behavioral VSTM capacity estimates of object identity and object spatial location that will display discrete neuroanatomical correlates. To explore this hypothesis, the subsequent data analyses were applied across the whole brain without any predefined domain specific anatomical segregation.

## MATERIALS AND METHODS

### Participants

A total of 48 healthy volunteers with normal or corrected-to-normal vision (aged 18–46, mean 24.73, SD = 5.78, 30 female) were recruited from the University College London subject pool. The local ethics committee approved all experiments and all participants gave informed consent.

### Stimuli and Apparatus

The experiment was controlled using the Cogent Toolbox (<http://www.vislab.ucl.ac.uk/cogent.php>) for Matlab (MathWorks) on a Lenovo PC running Microsoft Windows 7 attached to a 15" CRT monitor (90-Hz refresh rate). A viewing distance of 57 cm was maintained with a chin rest.

The memory set items were chosen from a pool of novel meaningless objects that subtended maximally  $1.5^\circ \times 1.5^\circ$ . Each item appeared in one of eight locations arranged in a circle ( $3^\circ$  in radius) around fixation. No item appeared in a previously used location in the same trial.

It was important to ensure that the VSTM tasks did not allow participants to rely on verbal working memory for successful performance in these tasks. For this reason, and to discourage participants from verbalizing the memory set items, we used a set of stimuli previously used by [Konstantinou et al., 2014]) that were created with a custom made MATLAB algorithm that generated meaningless symbols based on basic features of English angular letters (i.e., F, H, K, L, M, T, V, W, Y, and X). For each stimulus, the number of features was matched to the average number of bars used for each letter in Experiment 2a in Konstantinou et al., [2014]. All stimuli generated were individually screened, and any letters that resembled any specific English letter were excluded from the pool of stimuli. This process resulted in a set of letter-like stimuli that were novel and meaningless. To further discourage verbal rehearsal, we used an experimental paradigm that presented these stimuli in a rapid presentation paradigm (100 ms presentation time), that allowed very little time for naming each stimulus. These two measures thus ensured that participants relied mostly on spatial and object VSTM for successful performance on the spatial and object VSTM tasks, respectively.

### VSTM Task

As shown in Figure 1, each trial lasted for up to 5.8 s and consisted of fixation (1 s), eight sample displays with a duration of 100 ms each (total duration of the sample displays was 800 ms), blank delay interval (1 s), test display/response period (up to 3 s). An auditory tone (beep) was used as feedback for incorrect responses. Each memory-set item appeared randomly in one of the eight sample displays (e.g., in a trial with a set size of two items, each of the two items was randomly assigned to one of the eight sample displays and the remaining displays only contained a fixation cross). The fixation cross remained on the screen for the whole duration of the trial.

Participants were instructed to maintain the memory set items in VSTM throughout the retention interval by mentally projecting them on the screen visually, and not by verbalizing them. During the response period, participants used a button press to respond whether the memory probe item appeared at the same location as any of the memory set items for the spatial VSTM task or whether the memory probe item appearing at fixation was of the same identity as any of the memory set items. To minimize load on object VSTM, all items in the spatial memory set task were of the same identity.

### Staircase

The VSTM capacity of each participant was calculated using a 3-down/1-up adaptive staircase procedure. Specifically, following a short practice block of 12 trials, each participant completed an experimental block for each of

the spatial and the object VSTM tasks that started with a memory set size of two items. Following three consecutive correct-response trials, the memory set size was increased by one item in the following trial. Following an incorrect-response trial, the memory set size was decreased by one item. After 10 reversals of the staircase (a reversal was defined as any change in the direction of the staircase), the staircase was terminated. This procedure resulted in a group mean of 49 trials for the spatial VSTM task (SD = 9 trials) and a group mean of 45 trials for the object VSTM task (SD = 7 trials). Individual VSTM capacity estimates were calculated as the mean set-size at each of the last 8 staircase reversals.<sup>1</sup>

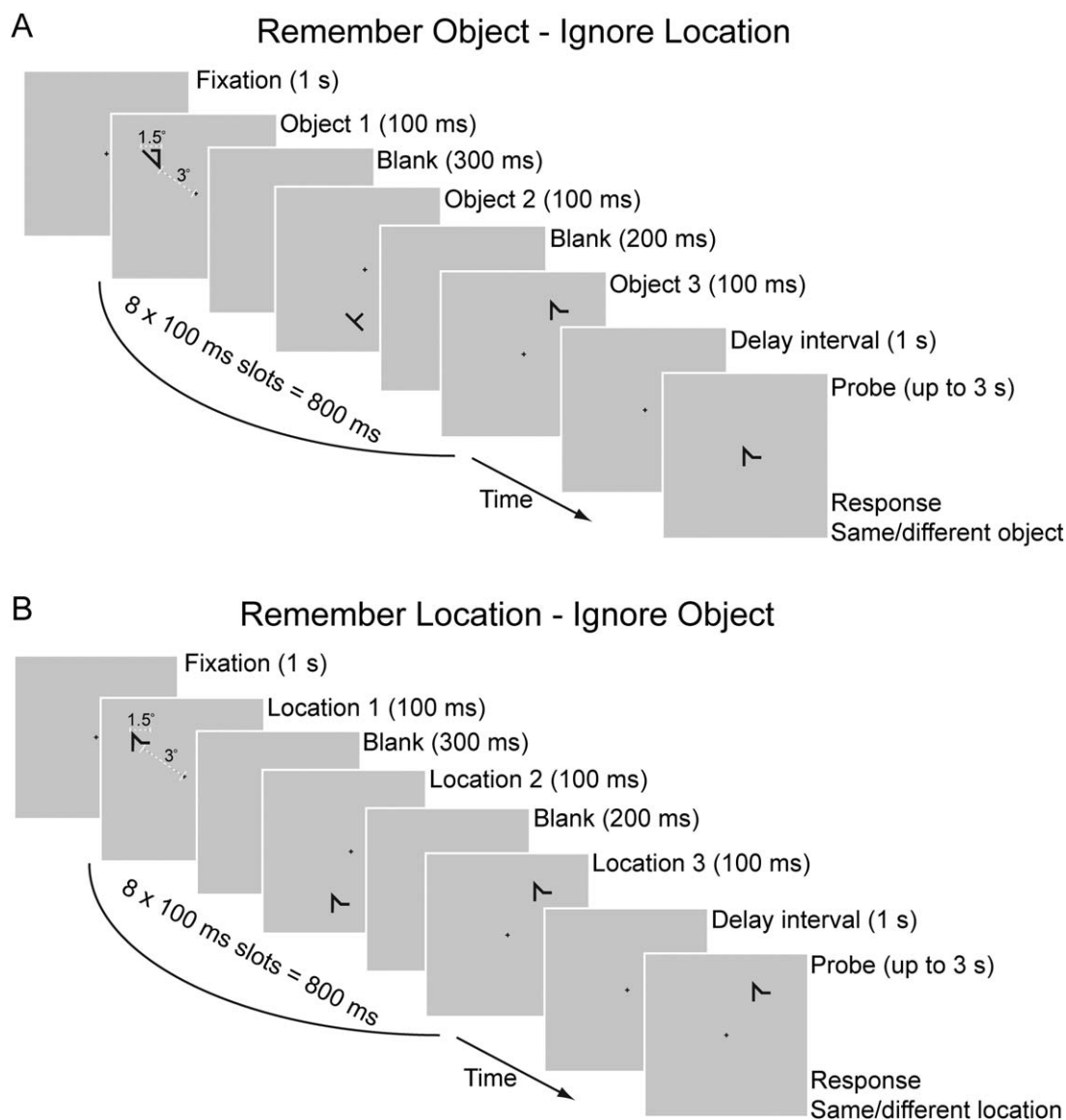
This method for estimating VSTM capacity presents some advantages over previous methods described above. Specifically, an adaptive staircase up/down method allows for rapid estimation of VSTM capacity minimizing the amount of effort required and fatigue over many trials, but also minimizing the effects of change in the observer's criteria. Previous studies attempting to estimate VSTM capacity based on Cowan's K [e.g. Konstantinou et al., 2012; Konstantinou and Lavie, 2013; Todd and Marois, 2004] were required to use a large number of trials (e.g. hundreds) for each memory set size [e.g. Luck and Vogel, 1997]. In up/down staircase methods, when an observer responds incorrectly to a trial, the stimulus intensity is increased (the equivalent of decreasing the memory set size) on the next trial, whereas if the observer responds correctly on a trial (or a short series of consecutive trials), stimulus intensity is decreased on the next trial (the equivalent of increasing the memory set size as was the case in this study). In such a procedure, the stimulus intensity level tends toward a specific proportion correct and oscillates around it once it is reached. Such adaptive methods, by adjusting the stimulus level to be used on each trial based on the responses to previous trials, increase efficiency and minimize fluctuations due to fatigue of participants over many trials [Kingdom and Prins, 2010; Taylor and Douglas Creelman, 1967].

### Image Acquisition and Analyses

MR images were acquired on a 1.5 Tesla Siemens Avanto MRI scanner (Siemens Medical, Erlangen, Germany) with a 32-channel head coil. High-resolution whole brain MR images were obtained using a T1-weighted three-dimensional magnetization-prepared rapid acquisition gradient-echo sequence (MPRAGE; repetition time = 2.73 s; echo time = 3.57 ms; voxel size = 1.0 × 1.0 × 1.0 mm).

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<sup>1</sup>The results pattern or significance did not change when the analysis was repeated using the mean of the last 10 reversals as the capacity estimate.



**Figure 1.**

Example trial sequence in the Object (A) and Spatial (B) VSTM conditions with a set size of three items. Note that the only difference between the two conditions is the requirement to maintain either only the object identity in A or only the locations of the objects in B. The correct response here is “same” for both examples. Stimuli are not drawn to scale.

### Voxel-Based Morphometry Preprocessing and Analysis

A whole-brain exploratory analysis using Voxel-based morphometry (VBM) was conducted with the aim of identifying GM voxels with significant correlation with the capacity estimates of spatial and object VSTM. The MR images were first segmented for GM and white matter (WM) using SPM8 (<http://www.fil.ion.ucl.ac.uk/spm>). A Diffeomorphic Anatomical Registration Through Exponentiated Lie Algebra

(DARTEL) in SPM8 was performed for intersubject registration of the GM images [Ashburner, 2007; Ashburner and Friston, 2000]. During this co-registration preprocessing, local GM volumes were conserved by modulating the image intensity of each voxel by the Jacobian determinants of the deformation fields computed by DARTEL. The registered images were smoothed with a Gaussian kernel (FWHM = 8 mm) and were then transformed to MNI stereotactic space using affine and nonlinear spatial

**TABLE I. Brain regions with a significant positive correlation between gray matter density and Spatial and Object VSTM capacity ( $P < 0.05$  uncorrected)**

Anatomical brain region	MNI coordinates of peak voxel			Cluster size (mm <sup>3</sup> )	Z	$P_{\text{uncorr}}$	$P_{\text{corr}}$
	X	Y	Z				
<b>Spatial</b>							
Left IPL (5I)	-31	-43	51	808	4.78	0.007	0.026
Left IPL (7PC)	-45	-45	55		4.33	0.007	0.026
Right IPL (hIP2)	52	-36	48	498	3.94	0.024	0.082
Right MFG	28	45	25	432	3.81	0.032	0.109
Right MFG	30	37	31		3.59	0.032	0.109
<b>Object</b>							
Left STG/insula	-36	-15	13	891	4.46	0.002	0.026
	-39	-13	3		3.77	0.002	0.026
	-44	-20	-3		3.28	0.002	0.026
Right STG/insula	40	-10	6	483	4.61	0.017	0.183
Right MOG	47	-77	12	299	3.89	0.051	0.461

Note.  $P_{\text{uncorr}}$ ,  $P$ -value for the cluster uncorrected;  $P_{\text{corr}}$ ,  $P$ -value for the cluster corrected for multiple comparisons; Z, z-score for peak voxel; IPL, inferior parietal lobule; MFG, middle frontal gyrus; STG, superior temporal gyrus; MOC, middle occipital gyrus. Cytoarchitectonic areas were found with SPM Anatomy toolbox [Eickhoff et al., 2005; Zilles and Amunts, 2010] and are shown in parenthesis.

normalization implemented in SPM8 for multiple regression.

The preprocessed images were entered into a series of multiple regression models in SPM8. A statistical threshold of  $P < 0.05$  corrected for the whole brain volume at a cluster level using the “Non-Stationary Cluster Extent Correction” toolbox for SPM (<http://fmri.wfubmc.edu/cms/NS-General>) [Hayasaka et al., 2004] was used as an indicator of regions of significant correlation between the VSTM capacity estimates and GM density. We aimed to identify cortical regions that showed correlations with each participant’s capacity estimate in the spatial and the object VSTM tasks. The design matrix included each participant’s spatial and object VSTM estimate, and the age and gender of the participant as covariates of no-interest. The total GM volume (for GM analyses) or total WM volume (for WM analyses) of each individual brain was also included in the design matrix to regress out any effect attributable to it.

Additionally, we have examined whether WM volumes underneath the regions identified by our primary GM analysis showed any relationship with the spatial and the object VSTM capacity. For this purpose, we first computed a  $T$  contrast with  $P < 0.001$  uncorrected as the criterion to detect voxels with a significant correlation. Then, we used small volume correction (SVC) in a sphere of 15 mm radius centered at the coordinates found in the GM analysis (see Table I) to identify WM regions that correlated with the spatial and the object VSTM capacity.

## RESULTS

### Behavioral Data

The individual VSTM capacity estimates of the spatial and the object VSTM tasks are presented in Figure 1. The

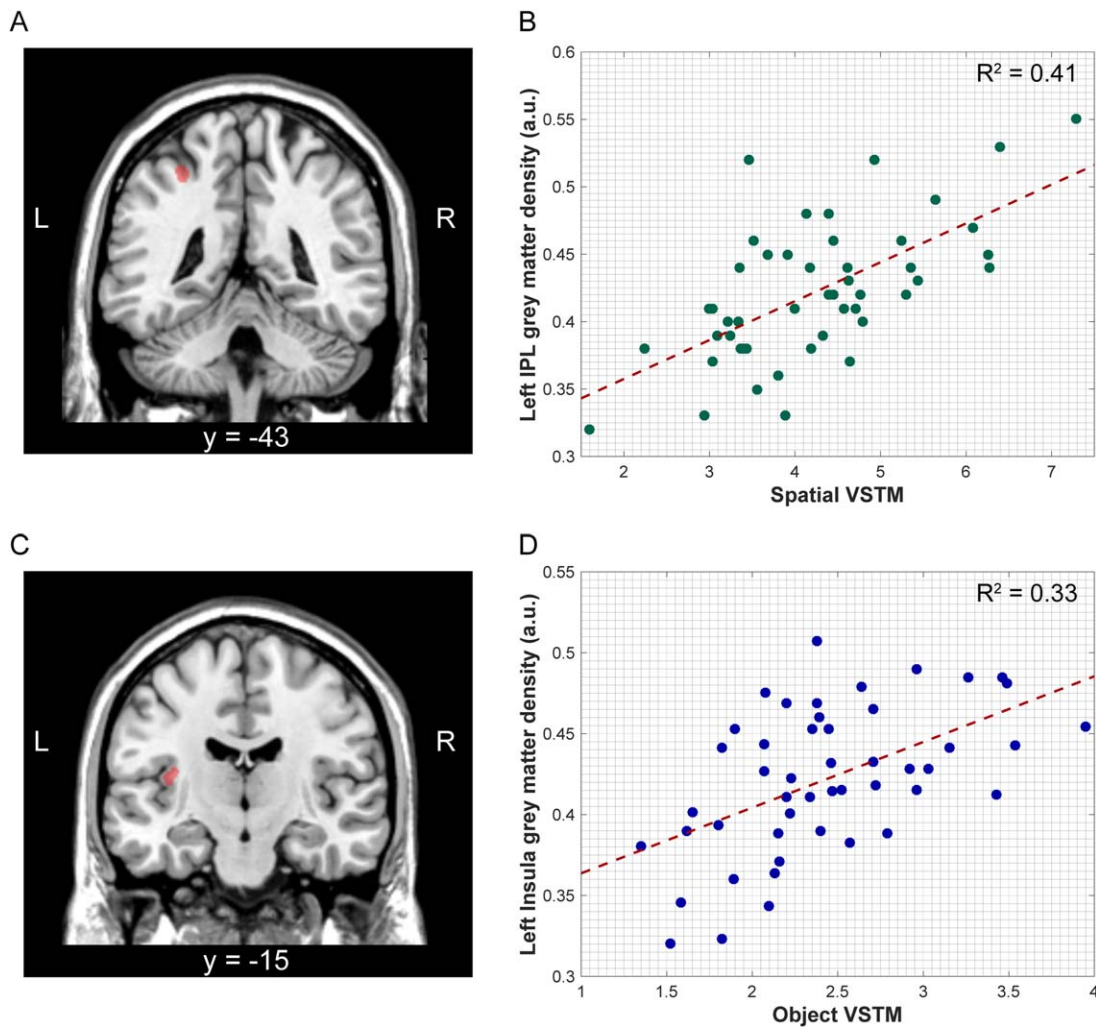
group mean capacity estimate for the object VSTM task was  $M = 2.44$  ( $SD = 0.59$ ), and for the spatial VSTM task  $M = 4.24$  ( $SD = 1.14$ ). The group mean accuracy rate for the object VSTM task was  $M = 79.36\%$  ( $SD = 2.27\%$ ), and for the spatial VSTM task was  $M = 82.41\%$  ( $SD = 2.50\%$ ).

Pearson product-moment correlation analysis was used to investigate the relationship between the behavioral capacity estimates of spatial and object VSTM. In line with our prediction of distinct VSTM capacity estimates of object identity and spatial location, this analysis indicated that the two capacity estimates are correlated with each other only weakly, and the correlation did not reach statistical significance,  $r(46) = 0.21$ ,  $P = 0.15$ .

### GM Analysis

VBM analysis was used to explore the correlations between local GM density and VSTM capacity. At the rigorous statistical threshold of  $P < 0.05$  corrected for multiple comparisons across the whole brain, significant correlations between GM density and spatial VSTM capacity were found in the left inferior parietal lobule (IPL;  $T(42) = 5.55$ ,  $P = 0.009$  FWE-corrected for the whole brain,  $z = 4.78$ ; Fig. 2). To assess the strength of this relationship, we extracted GM density at the peak voxels of the left IPL (centered at  $x, y, z$ , MNI coordinates:  $-31, -43, 51$ ) for each participant<sup>2</sup> and performed correlations with the individual spatial VSTM estimates, indicating a strong relationship,  $r(46) = 0.64$ ,

<sup>2</sup>The Shapiro–Wilk test of normality on the extracted individual GM density values from the peak voxels at the left IPL and the left insula indicated that the data come from a normal distribution (both  $P > 0.05$ ).



**Figure 2.**

Results of the GM voxel-based morphometry analysis. VSTM capacity estimates in the spatial task exhibited a positive correlation with GM volume in A) left IPL ( $x = -31$ ,  $y = -43$ ,  $z = 51$ ). B) The individual GM density of the peak voxel of the left IPL is plotted against individual spatial VSTM capacity estimates. C) Capacity estimates from the object VSTM task exhibited a

positive correlation with left Insula ( $x = -36$ ,  $y = -15$ ,  $z = 13$ ). D) The individual GM density of the peak voxel of the left insula is plotted against individual object VSTM capacity estimates. The lines in the scatterplots represent the best linear fit. L, left; R, right. [Color figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

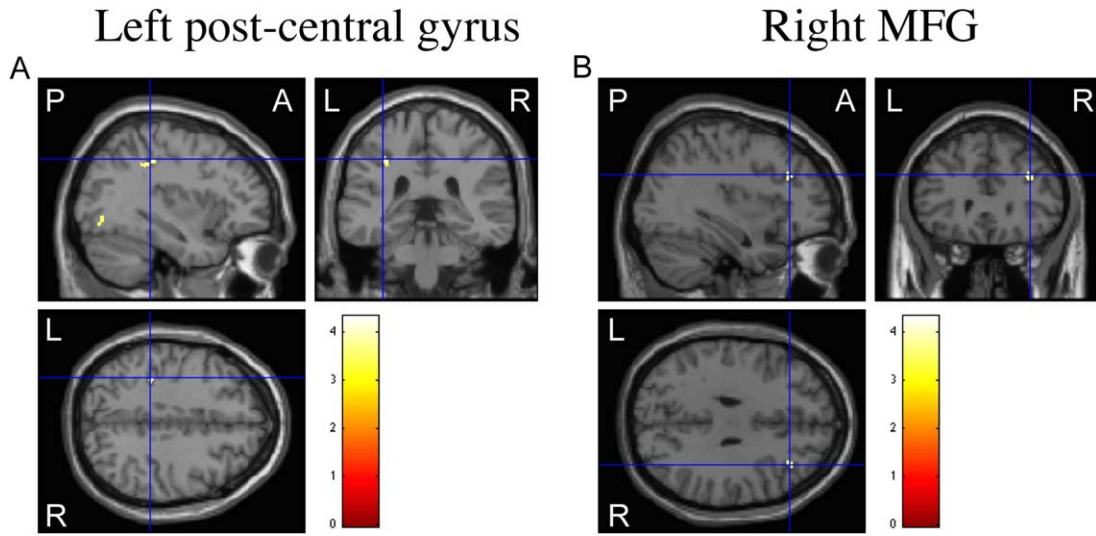
$P < 0.001$ .<sup>3</sup> Moreover, brain regions showing significant correlations between GM density and spatial VSTM capacity at a more liberal statistical threshold of  $P_{\text{uncorrected}} < 0.05$  were also found in the right IPL and right middle-frontal gyrus (MFG; see Table I).

As shown in Figure 2, object capacity estimates reached statistical significance with one cluster in the left insula at

the  $P < 0.05$  level corrected for multiple comparisons across the whole brain ( $T(42) = 4.90$ ,  $P = 0.026$ , FWE-corrected for the whole brain,  $z = 4.46$ ). Correlation analysis of GM density at the peak insula voxels (centered at  $x$ ,  $y$ ,  $z$ , MNI coordinates:  $-36$ ,  $-15$ ,  $13$ )<sup>2</sup> with individual object VSTM estimates indicated a strong relationship,  $r(46) = 0.57$ ,  $P < 0.001$ .<sup>3</sup> At a more liberal threshold of  $P_{\text{uncorrected}} < 0.05$  significant correlations were found with the right insula; right middle orbital gyrus approached significance (MOG; see Table I for full statistical details).

The findings from the more lenient statistical threshold of  $P_{\text{uncorrected}} < 0.05$  need to be interpreted with caution.

<sup>3</sup>Correlations tend to be overestimated at the peak voxels, and thus likely to be slightly inflated. For this reason, the strength of such relationships needs to be treated with caution [Kanai, 2016].



**Figure 3.**

White matter volume clusters exhibiting positive correlation using small volume correction with spatial VSTM capacity estimates in A) left postcentral gyrus ( $x = -34, y = -34, z = 42$ ), B) right middle frontal gyrus, MFG ( $x = 36, y = 30, z = 30$ ). A, anterior; P, Posterior; L, left; R, right. [Color figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

However, they are included here to facilitate the interpretation of the results in relation to previous findings as well as future work on this topic. No brain areas were found to be negatively correlated with either spatial or object VSTM capacity.

### WM Analysis

To examine whether GM correlates of object and spatial VSTM capacity are also reflected in the WM volumes underneath the same regions, we used SVC in a 15 mm sphere at the coordinates found in the GM analysis (see Table I and Methods for full details) to identify WM volume that showed a relationship with VSTM capacity estimates. We found that the WM volume of two clusters, one in the left postcentral gyrus and one in the right MFG were significantly correlated with spatial VSTM capacity estimates, as shown in Figure 3 (see Table II for full anatomical and statistical details). A further examination at a more lenient threshold in our volumes of interest from the GM analysis in Table I ( $P_{\text{uncorrected}} < 0.01$ ), and at a whole-brain corrected level ( $P_{\text{corrected}} < 0.001$ ) did not reveal any

regions that correlated significantly with the object VSTM capacity estimates.

### DISCUSSION

The current study investigated whether interindividual variability in VSTM capacity is reflected in the structure of the human brain. In line with the information segregation hypothesis, our findings demonstrated discrete behavioral capacity estimates for visual object information versus information about the spatial location of an object. These individual capacity estimates were associated with dissociable brain regions for object identity and object spatial location respectively. Specifically, the capacity for maintaining spatial locations in VSTM was predicted by regional GM volume in the left IPL, and WM volume in left postcentral gyrus and right MFG. Spatial VSTM estimates also exhibited a non-significant trend for positive correlations with GM in right IPL and right MFG. These findings are consistent with previous neuroimaging studies demonstrating neural activations during perception and short-term maintenance of spatial information in IPL [Chafee

**TABLE II. Brain regions with a significant positive correlation between white matter density and Spatial VSTM capacity estimate (SVC,  $P < 0.05$  FWE-corrected)**

Anatomical brain region	MNI coordinates			Cluster size ( $\text{mm}^3$ )	Z	P-value
	X	Y	Z			
Left postcentral gyrus	-34	-34	42	47	4.33	0.040
Right MFG	36	30	30	37	3.69	0.045

and Goldman-Rakic, 1998; Smith et al., 1995; Xu and Chun, 2009] and MFG [Goldman-Rakic, 1987; Leung et al., 2002; Levy and Goldman-Rakic, 1999; Esposito et al., 1999; Postle et al., 1999].

In contrast, VSTM capacity for visual information about the identity of the objects held in VSTM was predicted by the regional GM volume in the left insula. A non-significant trend for a positive correlation of the right insula and right MOG with object VSTM estimates was also found. Important, these brain areas that are distinct from those implicated in spatial VSTM, provide further support to the information segregation hypothesis.

Although the functions of the left insula, a brain area not generally considered as a part of the ventral visual stream, remain controversial [Bermudez-Rattoni, 2014; Jones et al., 2010; Kurth et al., 2010], our results are consistent with recent evidence demonstrating that the insula is differentiated into distinct functional regions. For example, a recent meta-analysis by Kurth et al. [2010] demonstrated that one of these insula regions (termed “the cognitive network”) has been shown to be consistently active in short-term memory tasks. This finding corroborates previous findings from both human and animal studies indicating that the insula is involved in object recognition memory by signifying objects that are novel [for a recent review, see Bermudez-Rattoni, 2014]. Moreover, in [Crinion et al., 2009], a region in the left insula (MNI coordinates,  $x, y, z$ :  $-36, -16, 2$ ) that corresponds to the left insula regions found in our study (see Table I) to be positively correlated with object VSTM estimates, was shown to exhibit greater gray and WM density in speakers of Chinese language.

Although our study was not designed to clarify the exact role of the left insula, we can nonetheless speculate, on the basis of such previous evidence taken together with our findings of significantly higher GM density in the left insula with higher VSTM estimates for our novel, meaningless letter-like visual objects, that the left insula may contribute to language processes through its involvement in short-term maintenance of complex visual objects such as letters and logograms.

Importantly, the dissociable findings between spatial and object VSTM rule out alternative accounts for the results in terms of limitations during the encoding stage and different strategies of allocating attention to the peripheral memory set stimuli. Because for both the spatial and the object VSTM tasks the memory set items required allocating attentional resources to the peripheral spatial locations for perceiving the items, any dissociable relationship with brain volume cannot be explained in terms of common (between the spatial and the object VSTM tasks) spatial attention strategies as it critically depended on whether the task required maintaining the spatial location or the object identity of the memory set items.

Previous research established a close link between inter-individual variability in visual perception and the

structure of visual cortex [Duncan and Boynton, 2003; Genç et al., 2015; Schwarzkopf and Rees, 2013; Schwarzkopf et al., 2011; Song et al., 2013]. More recently, Bergmann et al. 2016 demonstrated that the surface and thickness of primary visual cortex independently predict performance on a VSTM task. Our results extend these findings by demonstrating that the anatomy of brain areas previously implicated in perception and short-term maintenance of visual information can perhaps act as the bottleneck of our limited VSTM capacity. This is consistent with theories suggesting that the activity of parietal and prefrontal areas mediates our ability to maintain and manipulate information in working memory [Miller et al., 1991; Pessoa et al., 2002; Todd and Marois, 2004, 2005; Vogel and Machizawa, 2004; Xu and Chun, 2009]. Our findings are also consistent with a recent theory proposed by Franconeri et al. [2013] according to which our processing limits arise from the competition between individual memory items for cortical real estate, which according to our results exhibits a close relationship with individual VSTM capacity estimates.

Most previous research attempting to estimate the capacity of VSTM relied primarily on a visuo-spatial change-detection task that required observers to maintain information about an object’s identity (e.g. color or shape) as well as the object’s spatial location [Konstantinou et al., 2012; Konstantinou and Lavie, 2013; Luck and Vogel, 1997; Todd and Marois, 2004; Vogel et al., 2001]. For example, in the studies by Luck and Vogel [1997] and by Todd and Marois [2004] successful performance in the VSTM task critically depended on participants’ ability to maintain both the color and the location of each colored square. Consequently, estimates of VSTM capacity based on this task cannot distinguish between potentially distinct capacity limits and the associated neural correlates for object identity and object spatial location. Our results emphasize the importance of considering domain-specific VSTM capacity limits and challenge some of the most influential and enduring theories of attention and working memory suggesting general capacity limits that apply to all types of stimuli uniformly. For example, the influential multi-component model of working memory proposed by Baddeley and Hitch [1974] proposes a single short-term buffer, the visuospatial sketchpad, for maintaining and manipulating object information (e.g., shape, color) and spatial information (e.g., location, direction of movement).

However, working memory is not unitary and our findings provide a new line of support for the idea that during maintenance, the brain segregates visual information depending on the physical attributes of each piece of information (shape, orientation, color, motion, spatial location, etc.). Early neuropsychological and neuroimaging studies [Goodale and Milner, 1992; Haxby et al., 1991, 1994; James et al., 2003; Goodale and Milner, 1995; Newcombe and Ritchie Russell, 1969] provided evidence of object-spatial information segregation in the dorsal and ventral visual



pathways. More recent neuroimaging studies supported the hypothesis of object versus spatial information segregation during VSTM maintenance across the entire brain [Bellgowan et al., 2009; Buffalo et al., 2006; Cichy et al., 2011; Harrison et al., 2010; Mohr et al., 2006; Ranganath et al., 2004; Sala and Courtney, 2007; Sala et al., 2003]. Our findings of discrete domain-specific behavioral capacity limits and associated neuroanatomical correlates for object and spatial location provide novel behavioral and neural evidence in support of this dissociation.

The idea of information segregation during visual maintenance appears inefficient at first, as the brain needs to segregate information according to the nature of the information. However, it is now well established that after leaving the primary visual cortex, visual information is segregated in distinct pathways. For example, the ventral visual stream extending from the primary visual cortex to the temporal cortex specializes in object information processing, whereas the dorsal visual stream extending from the primary visual cortex to the parietal cortex specializes in spatial information processing. As the initial proposal by Schneider [1969] and Ungerleider and Mishkin [1982], the idea of information segregation has been supported by numerous lesion [Goodale and Milner, 1992; Ungerleider and Haxby, 1994], electrophysiology [Barash et al., 1991a, 1991b; Batuev et al., 1985; Chafee and Goldman-Rakic, 1998; Desimone et al., 1984; Fuster and Jervey, 1981; Gnadt and Andersen, 1988; Gross et al., 1972; Koch and Fuster, 1989; Miller et al., 1991; Miyashita and Chang, 1988; Sato et al., 1980], and histological studies in nonhuman primates [Andersen et al., 1985; Felleman and Van Essen, 1991; Kaas, 2003; Lyon, 2007]. Accordingly, the most efficient way by which to maintain visual information would be via activations of the same brain areas responsible for encoding and perceiving this information separately rather than merging the encoded information into combined representations. Indeed, previous research demonstrated that maintenance of visual information is associated with activity in the same brain areas that exhibited activity during perceptual encoding of the information [Bisley et al., 2004; Lee et al., 2005; Malecki et al., 2009; Munneke et al., 2010; Super et al., 2001]. This line of research provided evidence that competition between visual information held in memory and incoming visual information results in reduced sensitivity and visual cortex activity [Konstantinou et al., 2012], and that the pattern of activity during maintenance of visual information resembles the pattern associated with stimulus perception [Harrison and Tong, 2009; Serences et al., 2009]. Our findings extend these previous reports in now highlighting brain anatomy as a potential limiting factor and fit well with the recent findings of Cohen et al. [2014] who showed that working memory capacity limitations depend on the extent to which various stimuli are maintained by separate neural populations.

In summary, we have shown that people exhibit discrete behavioral VSTM capacity limits for object and spatial

information, which can be predicted by the structure of dissociable brain areas in the left Insula and left IPL respectively. Although the exploratory nature of this study requires independent replication of these results, these findings emphasize the need for considering domain-specific capacity estimates of VSTM and the importance of brain structure in acting as the bottleneck to VSTM, limiting the amount of information that the brain can maintain.

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