

## Visual working memory for simple and complex features: An fMRI study

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Visual working memory (VWM) allows us to hold visual information briefly in our minds after its disappearance. It is important for bridging the present to the immediate past. Previous neuroscience studies on VWM have shown that several parietal, frontal, and occipitotemporal brain regions subserved this function. Those studies, however, have often focused on VWM for a single property, such as color. Yet, in behavior, the capacity of VWM is sensitive to the complexity of to-be-remembered visual features. How do different brain areas represent VWM for visual features of different complexity and for combination of features? To address this question, we used functional MRI to study the response profile of several brain regions in three VWM tasks. In all tasks, subjects saw 1 to 7 colored polygons and had to remember their color (a simple feature), shape (a complex feature), or both color and shape. Behavioral performance showed that VWM reached capacity limit at about 3 colors, 2 shapes, and 2 compound objects. In the fMRI data, we found different functional profiles for frontal, parietal, and occipitotemporal regions. Specifically, the posterior parietal cortex was sensitive to both featural and VWM load manipulations. The prefrontal regions were sensitive to VWM load manipulation but relatively insensitive to featural differences. The occipitotemporal regions were sensitive to featural differences, but not to VWM load manipulation. We propose that the response properties of these regions can jointly account for several findings in human VWM behavior.

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### Introduction

Visual working memory (VWM) allows visual information to be retained momentarily after its disappearance (Logie, 1995). It maintains a sense of temporal continuity in a constantly changing

environment, allowing us to bridge the present to the immediate past. Previous studies using single-cell neurophysiology have revealed multiple brain regions important for VWM. Cells in prefrontal cortex show sustained activity during the delay period of a match-to-sample task, suggesting that they are important for creating a mental link between two temporal periods (Fuster, 1990; Goldman-Rakic, 1990; Miller et al., 1996; Rao et al., 1997). In addition, cells in posterior parietal, inferior temporal, and medial temporal cortices are also involved in VWM tasks, although their delay activity is less robust compared with that of the prefrontal neurons (Andersen et al., 1990; Miller and Desimone, 1994; Suzuki et al., 1997). Neuroimaging on normal humans provides converging evidence for the involvement of multiple brain regions in VWM tasks, including the prefrontal, parietal, and occipitotemporal cortices (D'Esposito et al., 1998; Marois and Ivanoff, 2005; Pessoa et al., 2002; Ranganath and D'Esposito, 2005; Ungerleider et al., 1998).

Different regions in the human brain also show different response properties in VWM tasks. Previous studies have focused on characterizing these differences. Early imaging studies showed that the posterior brain regions are organized based on the type of stimuli (spatial or nonspatial), with the occipitotemporal regions involved more in object VWM than spatial VWM and the posterior parietal regions involved more in spatial VWM than object VWM (Courtney et al., 1996; Owen et al., 1996; Ungerleider et al., 1998). This division between dorsal and ventral regions in spatial and nonspatial processing, however, was not observed in other studies, especially when the task required not just maintaining, but also monitoring of information in VWM (Dade et al., 2001; D'Esposito et al., 1998; Owen et al., 1998; Postle and D'Esposito, 1999).

Our study is designed to further test the similarities and differences among several brain regions in VWM tasks. We propose that a new way to characterize the functional roles of different brain regions is to focus on their response properties to different kinds of visual features (Munk et al., 2002). In particular, recent studies from human psychophysical literature have revealed three properties of human VWM. First, it is severely limited in capacity: only a few visual features can be retained in VWM simultaneously (Cowan, 2001; Jiang et al., 2000; Luck and Vogel,

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1997). Second, the exact capacity limit varies as a function of featural complexity. While we can retain about 4 simple features (e.g., color), we can only retain about 2 complex features (e.g., random shape; Alvarez and Cavanagh, 2004; Eng et al., in press). Third, the total number of features retained in VWM depends on whether these features are isolated or conjoined to form single objects. When people attempt to remember 4 colors and 4 orientations – a total of 8 features – they fail the task if the 8 features are presented as 8 isolated objects, but succeed at the task when the 8 features conjoin to form 4 colored bars (Luck and Vogel, 1997). Thus, human VWM is sensitive not only to VWM load (defined by the number of sample items), but also to featural complexity and how features are combined to form single objects. How different brain regions represent VWM load and featural differences can help characterize their functions.

Several neuroimaging studies have investigated effects of VWM load. For example, Druzgal and D'Esposito (2001) varied VWM load in an *N*-back task and found that both the fusiform face area and the prefrontal cortex are sensitive to VWM load. This finding was replicated in a later study by the same authors in an event-related study (Druzgal and D'Esposito, 2003), which allowed them to find differences in response timing between the fusiform and the prefrontal regions. Linden et al. (2003) varied VWM load in a modified match-to-sample task using novel shapes and found monotonic response function in some brain regions and U-shaped response function in others. Todd and Marois (2004) varied VWM load in a change detection task using colors and found a power or a linear response function in the brain as load increased. Because different brain regions showed different load-dependent activation patterns, these studies have been instrumental in characterizing VWM functions in the human brain (see also Jha and McCarthy, 2000). However, these studies are restricted to a single visual property – faces, shapes, or colors – and they have not compared VWM for different features.

In this study, we ask: how do different brain regions respond to features of different complexity and to conjunction of features? How does this response function interact with VWM load? To address these questions, we tested subjects in three VWM tasks using identical stimuli. Subjects were required to remember color,

shape, or both color and shape of colored polygons in different tasks. We also varied the VWM load from 1 to 7 items. Of interest is whether a given brain region is sensitive to VWM load, and whether this sensitivity changes for simple and complex features. We focus on several brain areas that have previously been implicated in VWM tasks: dorsal–medial prefrontal cortex, ventral–lateral prefrontal cortex, posterior parietal cortex, and occipitotemporal cortex. To our knowledge, this is among the first studies that have investigated VWM load and featural effects using neuroimaging (see also Munk et al., 2002; Xu and Chun, in press).

## Materials and methods

### Subjects

Twelve normal adults (1 male, 11 females; 18–31 years old) participated in this study for payment. All subjects gave written informed consent to participate in the study. Half of the subjects participated in Version A and the others participated in Version B. The two versions are described below.

### Task

#### Trial sequence

All subjects were tested in a modified change detection task (Rensink, 2002) in three conditions. In all conditions, subjects viewed colored random polygons on each trial. The sample display was presented briefly for 200 ms to discourage eye movement. This presentation duration was typically used in behavioral studies of VWM (e.g., Luck and Vogel, 1997); further increasing the duration can enhance VWM performance (e.g., Eng et al., in press), without changing effects of featural differences on VWM (Alvarez and Cavanagh, 2004; Eng et al., in press; Luck and Vogel, 1997). After a blank retention interval of 900 ms, a test display containing one probe item was presented. The subjects' task was to determine, within 1300 ms, whether or not the probe item was the same as the sample item presented at that location. Fig. 1 shows the sequence of a trial.

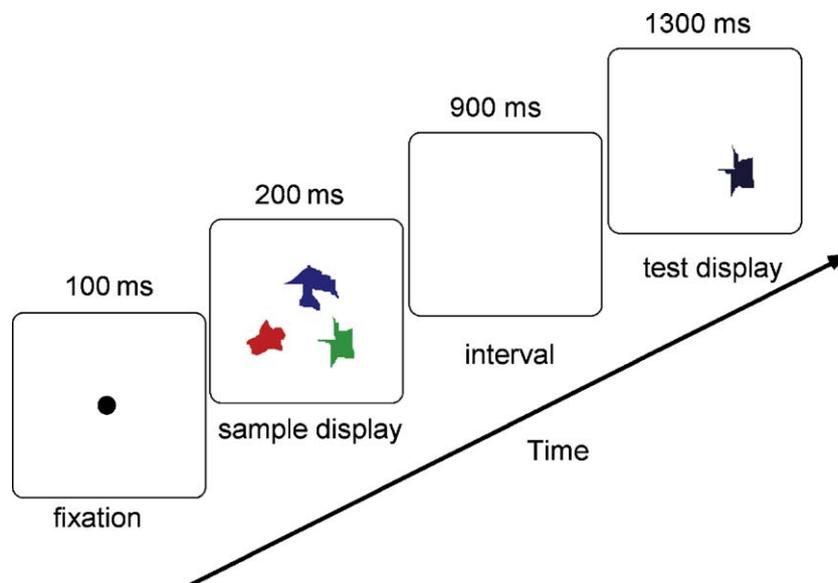


Fig. 1. An illustration of a trial sequence.

### Conditions

Subjects were tested in three feature conditions: *color-only*, *shape-only*, and *both*, in separate runs of a single scanning session. The conditions were similar except for task instructions. In the *color-only* condition, subjects were told to remember color and disregard shape. In the *shape-only* condition, subjects were told to remember shape and disregard color. The irrelevant dimension never changed from the sample to the test display. Finally, in the *both* condition, subjects were told to remember both color and shape. The test item changed on half of the trials. Whether it changed color or shape was randomly determined. Because subjects could not predict whether color or shape would later change in the *both* condition, they had to retain both properties in VWM. In all three conditions, the number of items (VWM load) on the sample array could be 1, 2, 3, 4, or 7. Different load was tested in different blocks in Version A, and randomly intermixed in Version B. The two versions of the experiment were otherwise similar.

### Display parameters

The sample display items were positioned randomly in an invisible  $3 \times 3$  matrix ( $7.5^\circ \times 7.5^\circ$ ). Each shape was generated by combining one of nine distinctive colors with one of nine random polygon shapes. No display contained two or more items of the same color or shape, and when a color or a shape changed, it always changed into a value not presented on the sample display. On half of the trials, the probe item was identical to the sample item at that position. On the other half of the trials, the probe item changed color (in the *color-only* condition), shape (in the *shape-only* condition), or either color or shape (in the *both* condition). Subjects pressed one of two keys to report whether they thought the probe was the same as the sample on the instructed dimension.

### fMRI procedure

After a 30-min practice session, subjects were scanned on a Siemens 3.0 T scanner with a standard head coil at the Martino's imaging center in Charlestown, MA. We first obtained a high-resolution structural scan of each subject's brain, and then tested subjects in 10–12 functional scans, depending on how many we could fit within a 1.5-h slot. The functional scans were collected using a standard T2\* weighted Gradient Echo scanning protocol, with standard scanning parameters (TE = 30 ms, flip angle =  $90^\circ$ ). We covered the whole brain except the bottom of the cerebellum with 30 contiguous axial slices (4 mm thickness). The in-plane spatial resolution was  $3.13 \text{ cm} \times 3.13 \text{ cm}$ .

### Functional scan composition

Each subject participated in 4 *color-only* scans, 4 *shape-only* scans, and 2 or 4 *both* scans. Within each scan, five different sample set sizes (1, 2, 3, 4, or 7) were tested, either in separate blocks (Version A) or in randomly mixed order (Version B).

**Version A (VWM load blocked).** For six participants, different VWM load was tested in separate blocks. Each scan lasted 4 min 56 s (TR = 2000 ms), which was divided into fixation blocks ('f') that lasted 16 s and task blocks ('T') that lasted 40 s (16 trials each for 2.5 s). Scans were run in sequences of fTfTfTfTfTf, and the five task blocks contained five different VWM loads. The order of the load was counterbalanced across different scans.

**Version B (VWM load randomized).** For the other six participants, the VWM load factor was randomly intermixed in presentation to minimize predictability. Each scan lasted 6 min 15 s (TR = 2500 ms), which contained 150 trials (each for 2.5 s). There were 25 trials for each of the 5 set size conditions and 25 fixation trials. The order of the presentation was randomized and optimized to allow maximal statistical power (Dale, 1999).

### Data analysis

#### Behavioral data

For each of the three feature conditions, we estimated the number of items held in VWM at different set sizes ( $N$ ) using Cowan's  $K$  (Cowan, 2001), where,

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

#### fMRI data

The fMRI data were analyzed using SPM99 and in-house regions-of-interest software. We first preprocessed the data, correcting for head motion, normalizing each subject's brain into a standard Montreal Neurological Institute (MNI) brain space, and spatially smoothing the data (FWHM = 8 mm).

Based on previous VWM studies, we selected 9 regions-of-interest (ROI). These ROIs were: in the *frontal* cortex: (1) left frontal eye field (L-FEF, MNI:  $[-27 \ -9 \ 48]$ , BA 6/8), (2) right frontal eye field (R-FEF, MNI:  $[30 \ -12 \ 51]$ , BA 6/8), (3) left inferior frontal sulcus (L-IFS, MNI:  $[-45 \ 0 \ 30]$ , BA 44), (4) right inferior frontal sulcus (R-IFS, MNI:  $[39 \ -3 \ 33]$ , BA 44), and (5) presupplementary motor area (pre-SMA, MNI:  $[12 \ 9 \ 51]$ , BA 6); in the *parietal* cortex, (1) left superior parietal lobule (L-SPL, MNI:  $[-24 \ -60 \ 48]$ , BA 7) and (2) right superior parietal lobule (R-SPL, MNI:  $[30 \ -60 \ 48]$ , BA 7); and in the *occipitotemporal* cortex: (1) left lateral occipital complex (L-LOC, MNI:  $[-48 \ -60 \ -21]$ , BA 37) and (2) right lateral occipital complex (R-LOC, MNI:  $[45 \ -63 \ -15]$ , BA 37). The center of the ROIs was determined based on a significant "Task > fixation" effect ( $P < 0.05$ , corrected for multiple comparisons). The radius of each ROI was 9 mm. Percent signal change (PSC) relative to the fixation baseline was calculated. In Version A, where a blocked-design was used, statistical power was relatively high, allowing us to treat each subject as a random factor in this analysis. An ANOVA on VWM load and feature condition was conducted across the 6 subjects. Percent signal change was calculated by averaging an entire block of a given VWM load. In Version B, where an event-related design was used, statistical power was relatively low (Desmond and Glover, 2002). In this case, we used a fixed-effect analysis by pooling data from all subjects. The fixed-effect analysis was justified given that Version B was a confirmation test of Version A. Percent signal change was calculated using the averaged peak responses that occurred at 2.5, 5, and 7.5 s after the onset of a trial.

## Results

#### Behavioral data

Accuracy in the VWM tasks declined with increasing VWM load. Table 1 shows the mean accuracy in each feature condition,

Table 1  
Mean accuracy in the VWM tasks (standard error in parenthesis)

Condition	Set size = 1	Set size = 2	Set size = 3	Set size = 4	Set size = 7
Color-only	0.97 (0.01)	0.95 (0.01)	0.90 (0.02)	0.82 (0.04)	0.70 (0.04)
Shape-only	0.97 (0.01)	0.89 (0.02)	0.79 (0.03)	0.70 (0.02)	0.56 (0.02)
Both	0.97 (0.01)	0.89 (0.03)	0.77 (0.04)	0.75 (0.02)	0.61 (0.02)

and Fig. 2 shows the estimated Cowan's  $K$  value. All statistical analyses were conducted on  $K$ , which is a measure of the number of items held in VWM at a given set size.

A repeated-measures ANOVA on feature condition (*color-only*, *shape-only*, or *both*) and VWM load (1, 2, 3, 4, or 7) as within-subject factor, and testing version (Version A or B) as between-subject factor revealed no effects of testing version (all  $F$ s < 1), suggesting that behavioral performance was insensitive to whether VWM load was blocked or randomly intermixed. There was a significant main effect of feature condition,  $F(2,20) = 17.12$ ,  $P < 0.001$ , in that  $K$  was higher for *color-only* than for *shape-only* ( $P < 0.001$ ) and higher for *color-only* than for *both* ( $P < 0.001$ ). The *both* condition was not significantly different from the *shape-only* condition ( $P > 0.30$ ). The main effect of VWM load was also significant,  $F(4,40) = 11.27$ ,  $P < 0.001$ , in that more items were held in VWM at higher set sizes. Finally, there was a significant interaction between feature condition and VWM load,  $F(8,80) = 6.54$ ,  $P < 0.001$ , suggesting that the number of items held in VWM reached plateau at different set sizes for different feature conditions.

In the *color-only* condition, Cowan's  $K$  increased significantly from set size 1 to 2 ( $P < 0.001$ ) and from 2 to 3 ( $P < 0.001$ ), but there was no statistical difference between set sizes 3, 4, and 7 ( $P$  values >0.20). Thus, Cowan's  $K$  saturated at about 3 sample items.

In the *shape-only* condition, Cowan's  $K$  increased from set size 1 to 2 ( $P < 0.001$ ), but there was no significant differences between set sizes 2, 3, 4, and 7 ( $P$  values >0.10). Cowan's  $K$  actually declined, although not significantly, from set size 4 to 7 ( $P > 0.10$ ). This decline was also seen in other capacity limited tasks. For example, in multiple-object-tracking, when the number of to-be-tracked objects exceeds capacity limit, subjects often lose track of *all* items rather than just the subset of items that exceeds capacity (Alvarez et al., 2004). This pattern of decline at high set sizes was also seen in *color-only* VWM tasks for low-capacity subjects.

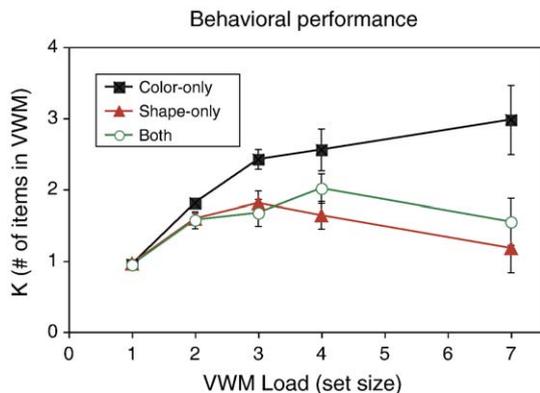


Fig. 2. Estimated number of items retained in VWM. Error bars show SEM between subjects.

Finally, in the *both* condition, Cowan's  $K$  increased from set size 1 to 2 ( $P < 0.001$ ), but there was no difference for set sizes 2, 3, 4, and 7,  $P$  values >0.10. Similar to the *shape-only* condition, performance declined marginally from 4 to 7 sample items,  $P > 0.07$ . Thus, subjects appeared to reach VWM capacity at about 3 items in the *color-only* condition, 2 items in the *shape-only* condition, and 2 items in the *both* condition. Note that although subjects had to remember both features in the *both* condition, performance was not worse than that in the *shape-only* condition. This finding is consistent with the idea that multiple features of a single object do not significantly compete for VWM capacity (Luck and Vogel, 1997; Olson and Jiang, 2002; Wheeler and Treisman, 2002).

In sum, our behavioral data are consistent with recent psychophysical studies on VWM. They show that (1) VWM is severely limited in capacity; (2) the exact limit varies with featural complexity, with higher capacity for simple features than complex features (e.g., 3 for color and 2 for shape); and (3) retaining multiple features of a single object is as easy as retaining a single feature of an object. What is the neural underpinning of these behavioral data? How do different brain regions respond to VWM load and featural manipulations? The fMRI data are presented below.

#### fMRI results

##### Version A: VWM load blocked

Of the 9 frontal, parietal, and occipitotemporal ROIs, 8 formed 4 pairs of corresponding locations on the left and right hemispheres, and 1 was near the mid-sagittal plane. Fig. 3 shows the mean percent signal change in each feature condition and VWM load, averaged across left and right hemispheres of a given region.

**Superior parietal lobule (SPL).** SPL has been implicated in VWM tasks (e.g., Owen et al., 1998; Postle and D'Esposito, 1999; Todd and Marois, 2004; Zarahn et al., 1999). We entered hemisphere (left or right), feature (*color-only*, *shape-only*, or *both*), and VWM load (1, 2, 3, 4, or 7) into a repeated-measures ANOVA. The main effect of hemisphere was not significant ( $F < 1$ ), nor did hemisphere interact with the other two conditions (all  $F$ s < 1.74,  $P$ s > 0.10). SPL activation was sensitive to VWM load manipulation,  $F(4,20) = 10.26$ ,  $P < 0.001$ , and to VWM featural complexity,  $F(2,10) = 9.93$ ,  $P < 0.004$ . The interaction between VWM load and feature condition, however, was not significant,  $F(8,40) = 1.65$ ,  $P > 0.10$ .

Follow-up ANOVA tests showed that activation in SPL increased marginally when VWM load increased from 1 to 2 ( $P = 0.06$ ), and significantly when the load increased from 2 to 3 ( $P < 0.001$ ), and from 3 to 4 ( $P < 0.05$ ). However, activation showed no increase from 4 to 7 ( $P > 0.20$ ). This pattern did not interact significantly with feature condition ( $P$  values >0.20), even though the overall activation level was lower for simpler feature (*color-only*) than for complex feature (*color-only* vs. *shape-only*,  $P < 0.001$ ; *color-only* vs. *both*,  $P < 0.06$ ).

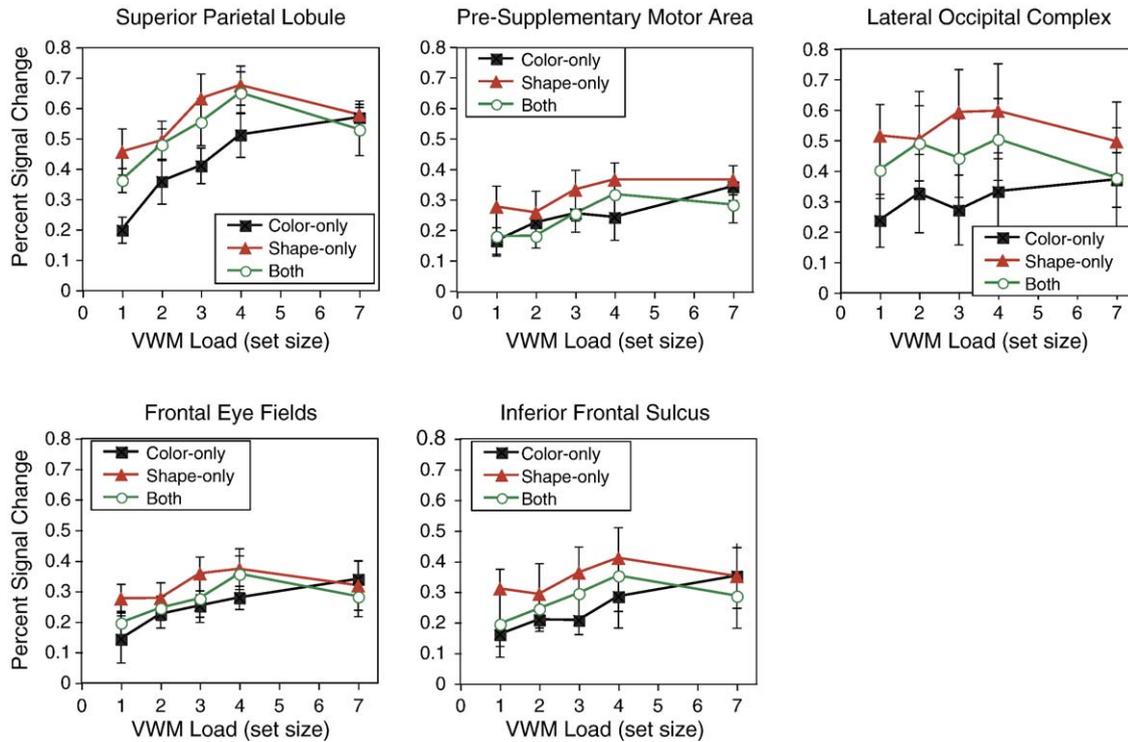


Fig. 3. fMRI results from Version A: effects of feature and VWM load. Error bars show SEM between subjects.

Compared with subjects' behavioral response pattern, SPL activation was similar to behavior in that its activation increased with heavier VWM load, and its activation was affected by featural complexity. Thus, SPL was involved in VWM tasks.

**Presupplementary motor area (pre-SMA).** Just like SPL, pre-SMA activation was sensitive to VWM load manipulation,  $F(4,20) = 9.61$ ,  $P < 0.001$ . However, activation in pre-SMA was not sensitive to the feature manipulation, with similar magnitude of activation for the *color-only*, *shape-only*, and *both* conditions,  $F(2,10) = 1.78$ ,  $P > 0.20$ . The interaction between VWM load and feature condition was not significant,  $F < 1$ . Thus, pre-SMA is sensitive to VWM load but not to the complexity of VWM features.

Follow-up ANOVA tests showed that activation in pre-SMA increased nonsignificantly from VWM load 1 to 2 ( $P > 0.10$ ), but significantly from VWM load 2 to 3 ( $P < 0.001$ ). Further increasing VWM load from 3 to 4 or from 4 to 7 did not affect pre-SMA activity (both  $F_s < 1$ ). The effect of load did not interact with feature condition ( $P_s > 0.20$ ).

**Lateral occipital complex (LOC).** Unlike SPL and pre-SMA, LOC was insensitive to VWM load manipulation. A repeated-measures ANOVA on hemisphere, feature, and VWM load revealed only a significant main effect of feature,  $F(2,10) = 18.17$ ,  $P < 0.001$ . No other main effects or interaction were significant ( $P_s > 0.10$ ). Follow-up ANOVAs showed no increase in LOC activity as the VWM load increased, all  $P_s > 0.25$ . As in SPL, LOC activity was lower in the *color-only* condition than in the *shape-only* condition ( $P < 0.001$ ) and the *both* condition ( $P < 0.03$ ).

**Frontal eye fields (FEF).** A repeated-measures ANOVA on FEF activity showed a significant main effect of VWM load,  $F(4,20) = 5.05$ ,  $P < 0.006$ , and a significant main effect of feature,  $F(2,10) =$

$7.70$ ,  $P < 0.009$ . The main effect of hemisphere was not significant,  $F < 1$ , nor were any interaction effects (all  $P_s > 0.45$ ). Like SPL, activity in FEF was higher for *shape-only* than for *color-only* condition ( $P < 0.02$ ) and intermediate for the *both* condition (*both* vs. *color-only*,  $P > 0.10$ ; *both* vs. *shape-only*,  $P < 0.01$ ). Activity increased nonsignificantly as VWM load increased from 1 to 2 ( $P > 0.20$ ), but significantly when VWM load increased from 2 to 3 ( $P < 0.05$ ) and from 3 to 4 ( $P < 0.05$ ). There was no significant difference between load 4 and 7 ( $P > 0.15$ ). The effect of VWM load did not interact with feature condition ( $P > 0.15$ ).

**Inferior frontal sulcus (IFS).** In IFS, there was a marginally significant main effect of hemisphere, with higher activation level on the right IFS,  $F(1,5) = 4.28$ ,  $P < 0.10$ , but hemisphere did not interact with the other effects ( $P_s > 0.30$ ). The main effect of feature did not reach significance,  $F(2,10) = 3.15$ ,  $P > 0.09$ . The main effect of VWM load was highly significant,  $F(4,20) = 7.90$ ,  $P < 0.001$ . Activation increased significantly when VWM load increased from 1 to 2 ( $P < 0.05$ ), from 2 to 3 ( $P < 0.05$ ), and from 3 to 4 ( $P < 0.07$ ). The difference between set sizes 4 and 7 was not significant ( $P > 0.15$ ).

Although the parietal, frontal, and occipital regions differ in the degree of sensitivity to VWM load and feature manipulations, it is important to note that as with behavioral data, null results – such as the lack of a load effect in LOC or a lack of a feature effect in pre-SMA – should be interpreted with caution. They should be considered in light of significant effects in other brain regions. To verify the difference across brain regions, we compared three regions that represented three different response profiles: SPL (sensitive to both feature and load), LOC (sensitive to feature but not load), and pre-SMA (sensitive to load but not feature). A significant interaction between region and feature confirmed that the three regions differed in their sensitivity to feature manipu-

lation,  $F(4,20) = 6.63$ ,  $P < 0.001$ . Furthermore, a significant interaction between region and VWM load confirmed that the regions differed in their sensitivity to VWM load,  $F(8,40) = 4.63$ ,  $P < 0.001$ . Thus, while we cannot claim a complete lack of load effect on LOC or a complete lack of feature effect on pre-SMA, their sensitivity is lower than that of other regions.

#### Version B: VWM load randomly intermixed

Because VWM load varied in different blocks, the load effect observed in Version A could reflect not only trial-by-trial differences in VWM load, but also sustained differences across blocks. Any sustained differences, if they existed, did not significantly change subjects' behavioral performance (see Behavioral data). Nonetheless, we examined the trial-by-trial load effect using an event-related design in Version B. Because the most clear featural difference in the blocked-design was observed between the *color-only* and *shape-only* condition, and because we only collected 2 scans of data from the *both* condition in the event-related design, here we focus on *color-only* and *shape-only* conditions.

**Superior parietal lobule (SPL).** Fig. 4 shows the hemodynamic response curves for the five ROIs, and Fig. 5 shows the set size function for peak activations. In SPL, an ANOVA on hemisphere (left vs. right), feature, and VWM load revealed only two significant effects: the main effect of feature,  $F(1,460) = 5.24$ ,  $P < 0.03$ , and the main effect of VWM load,  $F(4,460) = 5.08$ ,  $P < 0.001$ . No other effects were significant ( $F_s < 1$ ). Thus, similar to the blocked design data, SPL activation was sensitive to feature and to VWM load. Although SPL was sensitive to load, the exact shape of the load function in Version B was different from that shown in Version A. Follow-up tests did not find any of the adjacent set sizes to differ significantly from each other ( $P_s > 0.10$ ). There was, however, a significant linear trend of activation as load increased ( $P < 0.001$ ). Unlike behavior or results from Version A, activation did not appear to asymptote at 3 or 4.

**Presupplementary motor area (pre-SMA).** As in Version A, pre-SMA was sensitive to VWM load,  $F(4, 230) = 3.11$ ,  $P < 0.02$ , but not to feature,  $F(1,230) < 1$ . Activation increased linearly as load increased ( $P < 0.05$ ), again showing no obvious asymptote point.

**Lateral occipital complex (LOC).** In LOC, an ANOVA on hemisphere, feature, and VWM load revealed only a significant main effect of feature,  $F(1,460) = 15.55$ ,  $P < 0.001$ , all other  $F_s < 1$ . There was no significant linear or nonlinear relationship between LOC activation and load,  $P_s > 0.45$ . Thus, LOC was sensitive to feature differences but not to VWM load.

**Frontal eye fields (FEF).** Activation in FEF was significantly affected by hemisphere ( $P < 0.01$ ), with greater activation in the left FEF, but there were no interactions between hemisphere and other factors ( $F_s < 1$ ). FEF activity was sensitive to VWM load,  $F(4,460) = 2.95$ ,  $P < 0.02$ . Here, too, FEF activation increased linearly as load increased,  $P < 0.001$ . The main effect of feature, however, failed to reach significance,  $F < 1$ . Thus, the load effect shown in Version A was replicated, but the feature effect was not.

**Inferior frontal sulcus (IFS).** Similar to results from the blocked-design, the IFS was sensitive to VWM load,  $F(4,460) = 3.58$ ,  $P < 0.007$ , but not to feature ( $F < 1$ ). IFS activation increased linearly

as VWM load increased,  $P < 0.001$ . No other main effects or interaction was significant, all  $P_s > 0.20$ .

In summary, results from the event-related design were similar to the blocked design in some respects but different in others. In both designs, SPL was sensitive to feature and VWM load, pre-SMA and IFS were sensitive to VWM load but not to feature, and LOC was sensitive to feature but not to VWM load. FEF was sensitive to VWM load in both designs, and it was additionally sensitive to feature in blocked but not in event-related design. Although the two versions were largely similar in the sensitivity (or lack of sensitivity) to features and VWM load, they differed in the exact shape of the VWM load function. When VWM load was manipulated in a blocked-design, brain activation in SPL, pre-SMA, FEF, and IFS reached its peak at set size 4. It leveled off or dropped as set size increased further to 7. This pattern was true whether subjects had to remember color or shape. When VWM load varied randomly from trial to trial, brain activation in these regions increased linearly across the entire range of set sizes, with higher activation for set size 7 than for set size 4. Behavioral performance in both designs, however, showed an asymptote at intermediate set sizes, with no clear difference between designs.

The discrepancy between blocked design and event-related design may arise because subjects adopted different strategies in the two experiments. Because a VWM load of 7 items exceeded capacity, subjects could use two different strategies to perform the task. They could try to retain a subset of the items really well and ignore other items entirely, in which case the high load condition would be similar to an intermediate load condition. Alternatively, subjects could try to retain all items with each receiving a small fraction of the VWM capacity, in which case more locations must be monitored at higher load conditions. Performance would not change whether subjects monitored a subset of all items perfectly or monitored all items imperfectly, but brain regions sensitive to the spatial extent of monitoring (such as SPL and IFS, Culham et al., 2001; Jovicich et al., 2001) would show greater activity in the latter strategy. Randomly intermixing trials in an event-related design may promote subjects to adopt the second strategy. Future studies that directly manipulate encoding strategy are needed to test the validity of this proposal.

## Discussion

In this study, we obtained fMRI data from parietal, frontal, and occipitotemporal regions while subjects performed VWM tasks. We investigated how these brain regions react to different visual features, such as color, shape, or both, and to VWM load. Our study was motivated by recent psychophysical studies showing that the capacity of human VWM was sensitive to featural complexity and to how different features conjoin to form unified objects.

Consistent with previous VWM studies, we found that frontal, parietal, and occipitotemporal brain regions were involved in the VWM tasks. However, their functional profiles were different. Posterior parietal cortex was sensitive to both VWM load manipulation and to featural complexity. Activation increased as VWM load increased. This rising function was similar whether subjects were told to remember simple features (e.g., *color*), complex features (e.g., *shape*), or both. However, the overall magnitude of activation differed such that for an equal number of items, remembering shape, or both color and shape, produced greater activation than only remembering color.

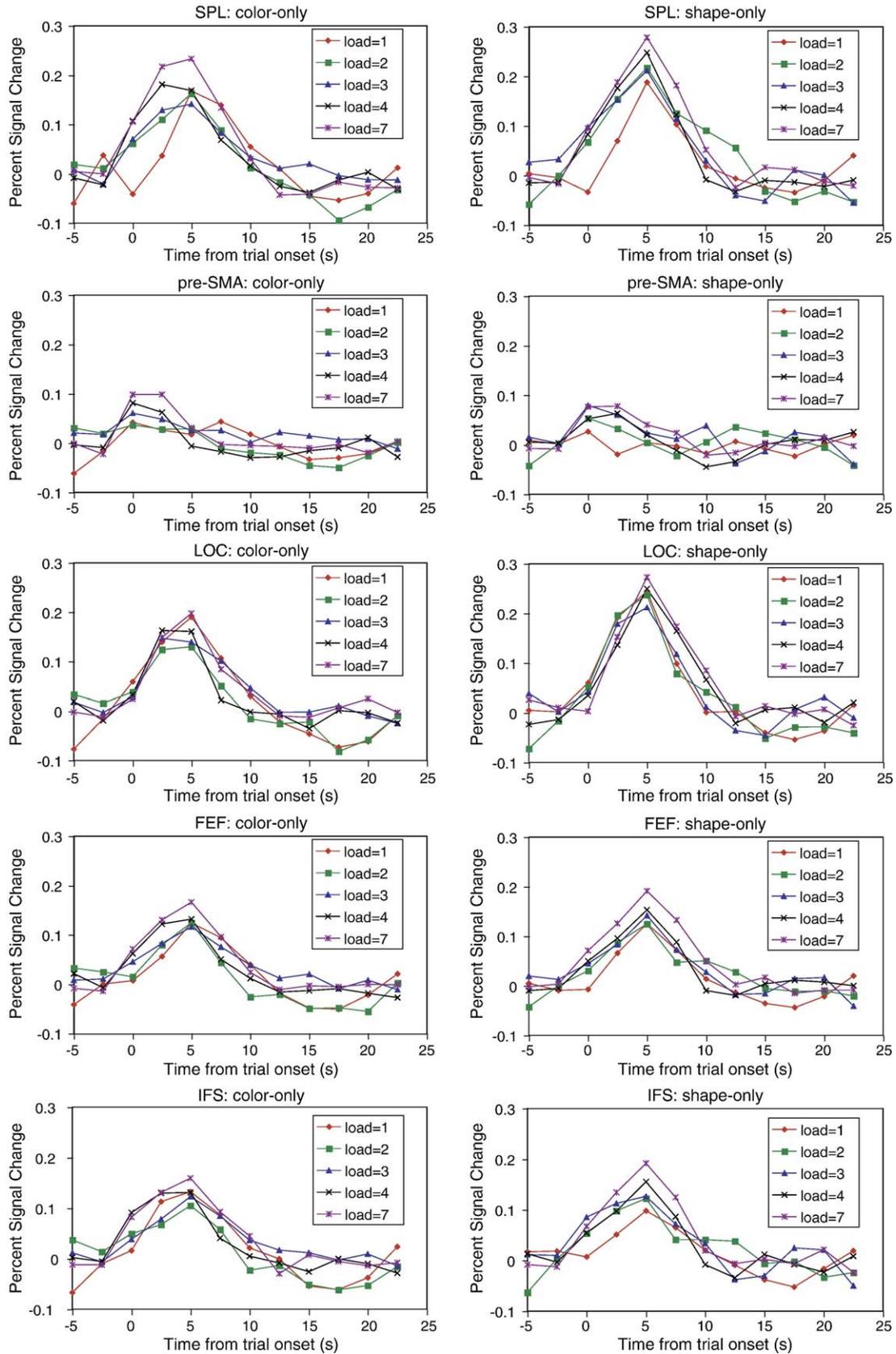


Fig. 4. fMRI results from Version B: effects of feature and VWM load.

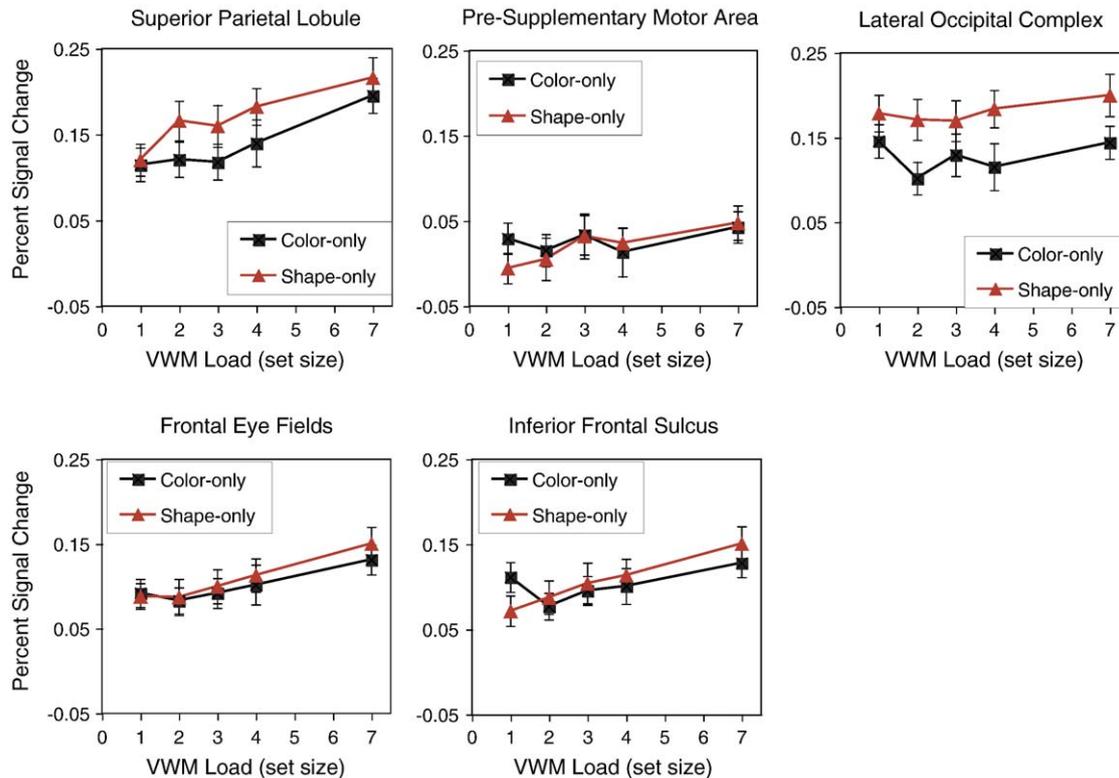


Fig. 5. fMRI results from Version B: effects of feature and VWM load. Error bars show SEM between subjects.

Unlike parietal regions, prefrontal regions such as pre-SMA and inferior frontal sulcus were relatively insensitive to the type of VWM features. These regions are sensitive to VWM load and also showed a monotonic increase in activation as VWM sample size increased. However, their activity was relatively unaffected by feature conditions. This is striking given that, at the behavioral level, the complexity of feature significantly changed performance. Thus, pre-SMA and IFS must be coding common factors across the feature tasks. It is likely that they represented the number of spatial locations or the number of individual objects involved in the task, but not the feature extracted from each location. This response profile is consistent with previous findings suggesting that pre-SMA and IFS are involved in spatial VWM (Courtney et al., 1998; Culham et al., 2001; D'Esposito et al., 1998). Currently, we cannot distinguish a space-based account from an object-based account. That is, we do not know whether pre-SMA and IFS track the number of separate locations or the number of isolated objects. Future studies that use overlapping locations of multiple objects may help address this question.

Unlike the parietal and frontal regions, the occipitotemporal region (LOC) was relatively insensitive to VWM load manipulation. Activation varied little as VWM load increased from 1 to 7, again a significant departure from behavioral performance. The lack of a load effect may seem inconsistent with previous studies that found a significant VWM load effect in occipitotemporal regions. For example, previous studies found that VWM load affected activity in the fusiform face area (Druzgal and D'Esposito, 2001, 2003) and the LOC (Linden et al., 2003). Most studies have interpreted the function of occipitotemporal cortex in terms of modulation by the prefrontal cortex (Miller et al., 1996). Because the strength of modulation likely correlates with the demand of VWM tasks, higher demand – induced by a greater VWM monitoring requirement (as is

the case in Druzgal and D'Esposito's *N*-back task) or by a longer delay period (as is the case in Linden et al.'s study) – can increase the involvement of occipitotemporal cortex in VWM tasks. In our study, VWM monitoring was similar across all set sizes and the retention interval was relatively short. These factors might have made LOC less sensitive to VWM load in our study than in other studies. LOC, however, was sensitive to featural differences, showing greater activation to shape VWM than color VWM. This is consistent with the role of LOC in coding object shapes (Grill-Spector and Malach, 2004; Kourtzi and Kanwisher, 2000).

Finally, activation in the FEF showed that this region was sensitive to VWM load, and the pattern of load effect did not interact with feature complexity. This observation suggests that just like SPL or pre-SMA, FEF is not directly involved in representing features in VWM, but in spatial monitoring of the task. The overall FEF activation was greater for shape VWM than color VWM in the blocked-design experiment, but this difference failed to reach significance in the event-related design experiment. Whether FEF is sensitive to feature complexity remains to be tested.

Our study used a short memory retention interval primarily because the paradigm stemmed from psychophysical studies. The benefit of using this paradigm is that one can easily compare our fMRI results with psychophysical studies (see also Druzgal and D'Esposito, 2001). In addition, as the retention interval lengthens beyond a few seconds, visual WM starts to decay and additional coding strategies, such as verbal WM, may contribute significantly to performance. However, because of the sluggish hemodynamic nature of the BOLD response, a short retention delay in fMRI does not allow us to separate different stages of VWM process, such as encoding, retention, and retrieval. However, this design feature does not invalidate our study, given that many neuroimaging studies have not shown clear separation

between encoding and mnemonic activity (Linden et al., 2003; Owen et al., 1998; Ungerleider et al., 1998), and that psychophysical studies have shown excellent correlation between encoding difficulty and VWM capacity (Alvarez and Cavanagh, 2004). Nonetheless, the best indicator of the VWM function is the delay activity in the brain. Future studies that use longer retention interval will help us isolate separate components of the VWM task.

When considered together, the five sets of brain regions investigated in this study can jointly account for seemingly conflicting theories in the psychophysical literature. Two broad classes of models have been proposed to characterize the capacity limitation of VWM. The *fixed-slot* model postulates that VWM is divided into a fixed number of about four slots, each slot corresponding to an individual visual object (Zhang and Luck, 2003). The object occupying each slot can vary in featural complexity. Alternatively, the *flexible-slot* model postulates that although VWM is limited in capacity, the division of this capacity into slots depends on the complexity of each object. For simple properties such as color, VWM may be divided into a large number of small slots, but for complex properties such as the shape of random polygons, VWM is divided into a small number of big slots (Alvarez and Cavanagh, 2004). Psychophysical studies have found different evidence for both hypotheses. In this study, for example, the greater capacity for color than for shape was consistent with the *flexible-slot* model, while the equivalent capacity for shape-only and color-shape combination was consistent with the *fixed-slot* model. Our fMRI data provide plausible neural instantiation for both models. Several regions, such as SPL, LOC, and possibly FEF, were sensitive to the complexity of features, with greater activation for shape than for color. Their activation is in part consistent with a *flexible-slot* model. On the other hand, pre-SMA and IFS were insensitive to featural complexity. Instead, they appeared to represent the number of spatial locations from which memory information must be extracted. Their activation was independent of what exactly must be extracted from those locations. This pattern is consistent with the *fixed-slot* model. Exactly how different brain regions cooperate to support human VWM behavior requires further investigation. Our study demonstrates that combining fMRI studies with behavioral research can advance our understanding of neural and cognitive mechanisms in VWM.

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