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**Research Articles: Behavioral/Cognitive**

**Parietal-occipital interactions underlying control- and representation-related processes in working memory for nonspatial visual features**

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Parietal-occipital interactions underlying control- and representation-related processes in  
working memory for nonspatial visual features

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**Abstract**

Although the manipulation of load is popular in visual working memory research, many studies confound general attentional demands with context binding by drawing memoranda from the same stimulus category. In this functional magnetic resonance imaging (fMRI) study of human observers (both sexes), we created high- versus low-binding conditions, while holding load constant, by comparing trials requiring memory for the direction of motion of one random dot kinematogram (RDK; 1M trials) versus for three RDKs (3M), or versus one RDK and two color patches (1M2C). Memory precision was highest for 1M trials, and comparable for 3M and 1M2C trials. And although delay-period activity in occipital cortex did not differ between the three conditions, returning to baseline for all three, multivariate pattern analysis (MVPA) decoding of a remembered RDK from occipital cortex was also highest for 1M trials and comparable for 3M and 1M2C trials. Delay-period activity in intraparietal sulcus (IPS), although elevated for all three conditions, displayed more sensitivity to demands on context binding than to load per se. The 1M-to-3M increase in IPS signal predicted the 1M-to-3M declines in both behavioral and neural estimates of working memory precision. These effects strengthened along a caudal-to-rostral gradient, from IPS0 to IPS5. Context binding-independent load sensitivity was observed when analyses were lateralized and extended into prefrontal cortex (PFC), with trend-level effects evident in left IPS and strong effects in left lateral PFC. These findings illustrate how visual working memory capacity limitations arise from multiple factors that each recruit dissociable brain systems.

**Significance Statement**

Visual working memory (VWM) capacity predicts performance on a wide array of cognitive and real-world outcomes. At least two theoretically distinct factors are proposed to influence VWM capacity limitations: an amodal attentional resource that must be shared across remembered items, and the demands on context binding. We unconfounded these two factors by varying load with items drawn from the same stimulus category (“high demands on context binding”) versus items drawn from different stimulus categories (“low demands on context binding”). The results provide evidence for the dissociability, and the neural bases, of these two theorized factors, and they specify that the functions of intraparietal sulcus may relate more strongly to the control of representations than to the general allocation of attention.

## 63 Introduction

64 Visual working memory (VWM) research has seen a convergence in recent years  
 65 between cognitive models emphasizing the role of attention to knowledge structures (Cowan,  
 66 1988, 1995, 1999) and neurophysiological evidence for the sustained engagement of circuits in  
 67 posterior cortex involved in the perception of the remembered information (Super et al., 2001;  
 68 Pasternak and Greenlee, 2005; Serences et al., 2009; Sprague et al., 2014; Foster et al., 2016; van  
 69 Kerkoerle et al., 2017). Among the outstanding questions about the precise mechanisms and  
 70 boundary conditions of this principle of “sensorimotor recruitment” in working memory (e.g.,  
 71 D’Esposito and Postle, 2015) is understanding the contributions to VWM of the territory of the  
 72 intraparietal sulcus (IPS) vis-a-vis classically defined visual circuits of occipital cortex.

73 A role for IPS in the short-term retention of egocentrically encodable spatial information  
 74 is well established (Chafee and Goldman-Rakic, 1998; Schluppeck et al., 2006; Hamidi et al.,  
 75 2008; Jerde et al., 2012). For nonspatial stimuli, however, the literature is more complicated.  
 76 Delay-period functional magnetic resonance imaging (fMRI) signal intensity is elevated in IPS  
 77 for even simple stimuli (e.g., motion directions (Riggall and Postle, 2012) or color patches (Todd  
 78 and Marois, 2004)), and varies with working memory load in a manner that can predict  
 79 individual differences in VWM capacity (Todd and Marois, 2004; Todd and Marois, 2005; Xu  
 80 and Chun, 2006), as do the dynamics of cross-frequency oscillatory synchrony localized to IPS  
 81 (Palva et al., 2010). Such load sensitivity could be consistent with a role in storage (Xu and  
 82 Chun, 2006; Xu, 2017) or in attentional control (Fukuda et al., 2015), or both. It is well  
 83 established that IPS contributes to the attentional control of visual perception (Anderson et al.,  
 84 2010; Scolari et al., 2015), as well as to the control of mnemonic stimulus representation, during  
 85 both stimulus encoding (Mitchell and Cusack, 2008, 2010; Weber et al., 2016) and retention

86 (Nelissen et al., 2013). Finally, efforts to decode stimulus identity from delay-period signal in  
 87 IPS has been uneven, with some successful (Christophel et al., 2012; Ester et al., 2015;  
 88 Bettencourt and Xu, 2016; Yu and Shim, 2017), some successful only under certain task  
 89 instructions (Sarma et al., 2016), and some unsuccessful (Linden et al., 2012; Riggall and Postle,  
 90 2012; Emrich et al., 2013; Lee et al., 2013).

91       Theoretical models of an amodal attentional resource hypothesized to constrain the  
 92 number of units or objects that have to be maintained in working memory (Cowan, 1995) have  
 93 drawn support from observations from the IPS. Common patterns of delay-period load-  
 94 sensitivity in IPS are observed for multiple stimulus modalities (Brahmbatt et al., 2008; Majerus  
 95 et al., 2010; Chein et al., 2011; Cowan et al., 2011), and multivariate pattern analysis (MVPA)  
 96 classifiers trained to discriminate high- from low-load conditions of VWM for colored squares  
 97 can successfully discriminate comparable conditions during working memory for visually  
 98 presented letters, and vice versa (Majerus et al., 2016). To date, however, many studies  
 99 employing load manipulations have used items drawn from the same category. This may  
 100 confound the effects of load, per se, with the possibly more specific control requirements of  
 101 managing the retention of multiple items drawn from the same category. Same-category memory  
 102 could entail more competition between items, leading to loss of precision, and can increase the  
 103 demands on context binding as proposed by many computational models (Oberauer and Lin,  
 104 2016; Schneegans and Bays, 2017) and generate “misbinding” (or “swap”) errors (Bays et al.,  
 105 2011).

106       The present study compared load manipulations for category-homogeneous (one vs. three  
 107 RDKs) versus category-heterogeneous (one RDK and two colors) memory sets, to address two  
 108 interrelated questions. First, can the general attentional demands of a load manipulation be

109 dissociated from the putatively more specific demands of the control of context binding? Second,  
 110 does load-sensitive activity in the IPS relate more closely to one or the other of these two  
 111 hypothetically dissociable types of top-down control?

112

## 113 **Materials and Methods**

### 114 *Subjects*

115 Twelve individuals (3 female, mean age 25 years (SD = 4), who reported normal or  
 116 corrected-to-normal vision, no history of neurological or psychiatric illness, and no  
 117 contraindications for fMRI were recruited from the local community. Recruitment and  
 118 experimental methods were approved by the University of Wisconsin–Madison Health Sciences  
 119 Institutional Review Board, and all subjects provided written informed consent.

### 120 *Stimuli and Procedure*

121 After training, subjects performed the delayed-recall task in the MRI scanner. Six blocks  
 122 of 30 trials (13 minutes each) were performed during concurrent fMRI, and an additional three  
 123 blocks of 24 trials (10 min 4 sec each) were performed during the same session, while the subject  
 124 was in the scanner, but without concurrent fMRI acquisition (more detail below).

125 The background of the projected image was black throughout each scanning session, and  
 126 each trial began with the onset of a white fixation mark (2 sec), which remained on the screen  
 127 until the trial-ending memory probe. Initial fixation was followed by the serial presentation of  
 128 three sample-display events. Each sample-display event comprised the 500 msec presentation of  
 129 a circular aperture subtending approximately 11° of visual angle, centered on fixation, and,  
 130 depending on the condition, filled with one of three types of stimulus: a field of stationary, low-  
 131 contrast gray dots (dot diameter ~0.13°; dot density ~0.07 dots/square degree); a field of high-



132 contrast white dots moving with 100% coherence at 2.75°/sec; or a uniform patch of color.

133 Although dots could move in any of the possible 360° of motion, on 90% of trials one was drawn

134 from the closed set of 7°, 127°, and 247° (to afford MVPA, as described below. During post-scan

135 debriefing, no subject reported noticing the recurring presentation of a small number of

136 directions), and the other two were selected at random. Colors were drawn at random, with

137 replacement, from a circular CIE L\*a\*b color space, with the constraint that no two sample items

138 presented on the same trial could be closer on the color wheel than 50°. The circle was centered

139 in the color space at (L = 70, a = 20, b = 38) with a radius of 60. Thus, colors had equal

140 luminance, and varied in hue and saturation. ISI between sample-display events was 250 msec.

141 The 2 sec of sample presentation was followed by an 8 sec delay period (white cross), then a

142 recall period of 5 sec, and finally 9 sec of ITI (total trial length of 26 sec).

143       There were three trial types: remember 1 direction of motion (“1M”); remember 3

144 directions of motion (“3M”); and remember 1 direction of motion and 2 colors (“1M2C”). On

145 1M and 1M2C trials, stimulus order across the three sample-display events was equiprobable and

146 unpredictable. For all three trial types, the recall stimulus was a dial of the same diameter and

147 location as the stimulus aperture, with a digit appearing in the center and a needle extending

148 from the digit to the circular edge of the dial. The digit (“1”, “2”, or “3”) corresponded to the

149 sample-display event that was to be recalled (the first, second, or third, respectively). For trials

150 requiring recall of the direction of motion, the circular edge of the dial acted as a “direction-of-

151 motion wheel”, and subjects adjusted the direction of the needle (via a trackball) to indicate their

152 memory of the direction of the probed sample, and pressed a button to register their response.

153 For trials requiring color recall, a color wheel appeared superimposed on the edge of the dial, and

154 subjects adjusted the needle to indicate their memory of the probed color (Figure 1). On all trials,

the starting position of the needle was randomly determined. On 3M and 1M2C trials, each stimulus had an equal probability of being probed. An equal number of trials of each type occurred, in an unpredictable order, during each of six 30-trial runs. This design allowed us to compare the effects of a manipulation of load on VWM for motion, when the two additional items on load-of-3 trials were drawn from the same or different stimulus domains.

Note that, because memory for each item on 1M2C trials was probed an equal number of times, those performed during fMRI scanning yielded only 1/3 as many instances of recall of motion as did the other two trial types. In order to acquire a sufficient number of motion-probed 1M2C trials to fit to a mixture model (described in Behavioral analyses), an additional 24-trial block was performed by each subject prior to the first and fourth scanned block, and immediately after the sixth one. Each block of these supplementary behavioral trials contained 24 1M2C trials (randomly ordered), and half of these 1M2C trials probed the RDK and half probed a color. This yielded an additional 36 motion recall trials that were combined with the 18 from the fMRI session to yield a total of 54 1M2C trials that were entered into the mixture model.

The behavioral experiment was administered via the Psychophysics Toolbox (<http://psychtoolbox.org>) running in MATLAB (MathWorks), presented using a 60 Hz projector (Avotec Silent Vision 6011), and viewed through a coil-mounted mirror in the MRI scanner. An fMRI-compatible trackball fiber optic response pad (Current Designs Inc., HHSC-TRK-2) was employed to record the behavioral responses.

#### *Behavioral analyses*

As with Emrich, Riggall, et al. (2013), we used this delayed-recall (a.k.a. “delayed estimation”) procedure in order to estimate the precision of mnemonic representations by fitting response error to a three-factor mixture model. The model (Bays et al., 2009), implemented with

code available from <http://www.bayslab.com>, uses maximum likelihood estimation to generate estimates of 1) the proportion of responses based on a working memory representation of the probed item (“responses to target”); 2) the proportion of responses incorrectly based on a representation of an unprobed item (i.e., “misbinding” or “swap” errors); and 3) the proportion of responses that were guesses not based on any working memory representation, and 4) a “concentration” parameter that estimates the precision of target responses (i.e., that is based on the distance between the true target position and the subject’s response, for the set of responses estimated to have come from categories 1 and 2). Conceptually, the concentration parameter is similar to a model-free measure of the precision of responses that is computed as the inverse of the standard deviation of the distribution of responses. It is taken as a proxy for the fidelity of the working memory representation. Reaction time of the response-ending button press was also collected, although this measure was necessarily noisy because it included the time to adjust the response dial with a trackball positioned adjacent to the thigh of the supine subject.

#### *fMRI Data acquisition*

Subjects were in a comfortable supine position, and wore earplugs and headphones. Whole brain images were acquired using a 3 Tesla GE MR scanner (Discovery MR750; GE Healthcare) at the Lane Neuroimaging Laboratory at the University of Wisconsin–Madison HealthEmotions Research Institute (Department of Psychiatry). Blood oxygen level-dependent (BOLD) data were acquired with a gradient-echo planar sequence (2 sec repetition time (TR), 25 msec echo time (TE), 60° flip angle) within a  $64 \times 64$  matrix (39 sagittal slices, 3.5mm isotropic). Each of the six fMRI scans generated 390 volumes. A high-resolution T1 image was also acquired for all subjects for coregistration to the functional data with a fast spoiled gradient-

200 recalled-echo sequence (8.2 msec TR, 3.2 msec TE, 12° flip angle, 160 axial slices, 256 × 256  
 201 in- plane, 1.0 mm isotropic).

## 202 *fMRI Data Preprocessing*

203 We preprocessed the functional data using the Analysis of Functional NeuroImages  
 204 (AFNI) software package (<http://afni.nimh.nih.gov>; Cox, 1996). For each subject's data, all  
 205 volumes were spatially aligned to the final volume of the last functional run, then to the  
 206 structural volume. The preprocessing steps were slice-timing correction, detrending, conversion  
 207 to percent signal change, and spatial smoothing with a 4-mm FWHM Gaussian kernel.

## 208 *Univariate analyses*

209 We calculated the percent signal change in BOLD activity relative to baseline for each  
 210 time point during the working memory task; baseline was chosen as the average BOLD activity  
 211 of the first TR of each trial. A conventional mass-univariate general linear model (GLM)  
 212 analysis was implemented in AFNI, with sample, delay and probe periods of the task modeled  
 213 with boxcars (2 sec, 8 sec, and 5 sec in length, respectively) that were convolved with a  
 214 canonical hemodynamic response function.

## 215 *ROI definition*

216 Much of the motivation for the present study came from the fact that we have previously  
 217 observed different patterns of activity, consistent with the operation of distinct cognitive  
 218 operations, in different parts of the brain. In particular, in a task requiring VWM for one vs. two  
 219 vs. three RDKs, successful MVPA decoding of delay-period stimulus information, consistent  
 220 with a storage function, was primarily observed in occipital cortex, whereas load-sensitive  
 221 variation in BOLD signal intensity, perhaps reflecting a control operation, was observed in IPS,  
 222 as well as in regions of PFC (Emrich et al., 2013). Therefore, our a priori hypotheses were tested

223 in functionally-defined, anatomically constrained ROIs based theoretically on past work. These  
 224 ROIs allow the most powerful examination of the hypotheses, given individual differences in  
 225 brain anatomy. However, given that functional ROIs are necessarily biased by the voxel  
 226 selection procedure, we also developed anatomical ROIs, motivated by past work, to ask more  
 227 general, nomothetic questions about areas of the cortex.

228       The principal hypothesis tests were carried out in two anatomically constrained  
 229 functional ROIs: an *Occipital Sample* ROI intended to capture regions previously associated with  
 230 the delay-period retention of stimulus representations; and a *Parietal Delay* ROI intended to  
 231 capture regions of IPS previously shown to demonstrate delay-period load sensitivity of BOLD  
 232 signal intensity (Emrich et al., 2013). The *Occipital Sample* ROI was defined as the 2000 voxels  
 233 displaying the strongest loading on the contrast [sample - baseline] from the GLM, collapsed  
 234 across the three conditions, and located within an anatomically defined occipital ROI (see  
 235 below). The *Parietal Delay* ROI was defined as the 2000 voxels displaying the strongest loading  
 236 on the contrast [delay - baseline], also collapsed across the three conditions, and located within  
 237 an anatomically defined IPS ROI. In effect, the [sample - baseline] and [delay - baseline]  
 238 contrasts served as the basis for feature selection for the MVPA that we planned to carry out in  
 239 the occipital cortex and IPS, respectively.

240       Occipital and parietal anatomical ROIs were created by extracting masks for V1-V4,  
 241 V3a, V3b, and LO, and for IPS0-IPS5, respectively, from the probabilistic atlas of Wang and  
 242 colleagues (2015), and warping them to each subject's native space. Based on the results from  
 243 occipital and parietal ROIs, we followed-up with additional analyses performed in the left  
 244 hemisphere half and the right hemisphere half of the *Parietal Delay* ROI, and in the prefrontal  
 245 cortex with a *Lateral PFC Delay* ROI comprising the 2000 voxels with the strongest loading on

the contrast [delay - baseline], collapsed across the three conditions, and located anatomically within a region defined by the union of masks of the superior, middle, and inferior frontal gyri supplied by AFNI. This *Lateral PFC Delay* ROI was also divided into a left hemisphere half and the right hemisphere half.

#### *Pattern classification*

Multivariate pattern classification was performed using the Princeton Multi-Voxel Pattern Analysis toolbox ([www.pni.princeton.edu/mvpa/](http://www.pni.princeton.edu/mvpa/)). The 10% of trials that did not include one of the three critical directions of motion, as well as the first and last trials of each run, were discarded from further analysis. We used L2-regularized logistic regression with a penalty term of 25 to classify the three critical motion directions. Specifically, the classifier was trained and tested on the three motion directions at each time point through a leave-one-trial-out k-fold cross-validation procedure. The training dataset was collapsed across all three trial types. For each iteration, an estimate (ranged from 0 to 1) of the similarity between the pattern on the test trial and the training pattern (a.k.a., MVPA “evidence”, c.f. Lewis-Peacock and Postle, 2012) was generated for each of the three motion directions. Classification performance was characterized by the difference between the evidence for the target motion direction relative to the mean of the evidences for the two non-target motion directions, and averaged across trials within each condition. Classifier performance values higher than 0 indicated higher sensitivity for the correct motion direction, compared with the incorrect motion directions.

Of primary theoretical interest was the item-level classification of stimulus motion direction (7° vs. 127° vs. 247°). Additionally, however, we also planned to carry out category-level MVPA to assess the discriminability of activity related to the trial type (1M vs. 3M vs. 1M2C).

269 *Task-related patterns of covariation*

270       Following our previous work (Emrich et al., 2013), we used analysis of covariance  
 271 (ANCOVA) to evaluate evidence for correlated sensitivity to trial type (e.g., 1M vs. 3M) across  
 272 pairs of dependent variables (i.e., permutations of BOLD loading on covariates from the GLM  
 273 analyses [a.k.a. “beta values”] vs. classification performance vs. behavioral precision). Unlike  
 274 simple correlations, ANCOVA accommodates the fact that each subject contributes a value for  
 275 each level of the factor of trial type. It removes between-subject differences and assesses  
 276 evidence for “within-subject correlation”: the extent to which remaining variation in one  
 277 dependent variable can be explained by variation in a second (Bland and Altman, 1995).

278       Instead of modeling trial epochs across trials, as we did when defining the Sample and  
 279 Delay ROIs, we modeled the sample, delay, and probe periods on a trial-by-trial basis (still using  
 280 boxcar regressors of 2 sec, 8 sec, and 5 sec, respectively) in order to better capture the fluctuation  
 281 in BOLD activity between trials. Classification performance for these analyses was calculated  
 282 across the average signal from 10-14 sec after trial onset; behavioral precision was defined as the  
 283 concentration parameter in the mixture model. First, to test for replication of the finding that  
 284 load-related changes in MVPA predict load-related changes in behavioral precision (Emrich et  
 285 al., 2013), we performed an ANCOVA of classification performance in the *Occipital Sample*  
 286 ROI vs. behavioral precision, across 1M and 3M trial types. Next, assuming successful  
 287 replication, to assess whether this effect is related to memory load, per se, or, rather, to the  
 288 additional control demands imposed by stimulus homogeneity, we repeated this analysis, but  
 289 across the trial types 1M and 1M2C (All subsequent analyses were also performed separately for  
 290 1M vs. 3M and for 1M vs. 1M2C). A second set of ANCOVAs was planned to examine, at each  
 291 ROI, whether load-sensitive patterns of delay-period BOLD activity related to load-sensitive

292 patterns of behavioral precision. Finally, to further investigate evidence for parietal control of  
 293 working memory representation (Mitchell and Cusack, 2008, 2010; Nelissen et al., 2013; Weber  
 294 et al., 2016), a third set of ANCOVAs, one at each IPS ROI, was planned to assay relations  
 295 between parietal BOLD activity and occipital MVPA performance.

#### 296 *Experimental design and statistical analysis*

297       The experiment was a within-subject design of three trial types: 1M, 3M, and 1M2C.  
 298 Tests of changes across three trial types, and across ROIs, were performed using one-way  
 299 repeated-measures analysis of variance (ANOVA). Tests of difference between two conditions  
 300 were performed using paired two-tailed *t*-tests. Tests of difference between one condition and 0  
 301 were performed using one-sample two-tailed *t*-tests. Bonferroni correction was applied to all  
 302 pairwise comparisons, unless specified otherwise. Evaluation of within-subject correlations  
 303 (ANCOVAs) was described in the section above.

304       In addition to this frequentist statistical reporting, we also estimated Bayes factors for  
 305 each of the comparisons. The Bayes factor can be understood as the ratio of the likelihood of the  
 306 alternate hypothesis compared with the null hypothesis. For the Bayes factors, values >1 indicate  
 307 greater evidence in favor of the alternative hypothesis (i.e., that decoding was successful), and  
 308 values < 1 indicate greater evidence in favor the null hypothesis (i.e., that decoding was  
 309 unsuccessful, implying that there is no stimulus information in that ROI). Bayes factors allow for  
 310 the quantitative assessment, for each effect in each ROI, of the strength of evidence in favor of  
 311 the null versus the alternative hypothesis. In this analysis, we chose the simplest possible prior  
 312 distribution for the Bayes factor analysis, which is a uniform distribution from 0 to the maximum  
 313 possible classification performance value (which we set to 0.35, a value 0.01 higher than the  
 314 highest classification performance achieved in any subject's data, in the *Occipital Sample* ROI).



315

316 **Results**317 *Behavior*

318       The (model-free) descriptive statistics suggested that task difficulty increased from 1M to  
 319 1M2C to 3M, as reflected in the distribution of response error (converted to “precision” as  $1/SD$   
 320 of error,  $F(2,22) = 7.07$ ,  $p = 0.004$ ; and as reflected in RT,  $F(2,22) = 16.05$ ,  $p = 5 \times 10^{-5}$ ; Table  
 321 1).

322       Results from mixture modeling indicated no differences across trial types in the  
 323 probabilities of target responses, of non-target responses, or of guesses (all  $ps > 0.148$ ; Table 1).  
 324 The concentration parameter, which provides an estimate of the precision of mnemonic  
 325 representations, was significantly higher for 1M trials than for both 3M trials ( $t(11) = 10.56$ ,  $p =$   
 326  $0.021$ ) and 1M2C trials ( $t(11) = 11.83$ ,  $p = 0.046$ ), but did not differ between 3M trials and  
 327 1M2C trials ( $t(11) = 0.13$ ,  $p > 0.999$ ).

328 *Univariate delay-period activity*

329       BOLD activity in the *Occipital Sample* ROI decreased steadily after the stimulus-evoked  
 330 response, dropping to baseline by time 12 sec. Moreover, activity in the 3M condition was higher  
 331 than the other two conditions during the very early delay period, but it didn’t differ at later delay  
 332 time points across any of the three conditions (Figure 2A). Comparisons between average delay-  
 333 period activity (10-14 sec) further confirmed no difference between any two of the conditions, all  
 334  $p > 0.132$ .

335       In the *Parietal Delay* ROI, in contrast, one-sample t-tests against 0 at each time point  
 336 confirmed that delay-period activity was elevated in a sustained manner for all the three  
 337 conditions. Furthermore, although delay-period activity in the 3M condition was significantly

338 higher than in the two other conditions, it did not differ between the 1M and the 1M2C  
 339 conditions (Figure 2B). Average delay-period activity (10-14 sec) in the 3M condition was also  
 340 significantly higher than the other two conditions,  $t(11) = 7.95$  and  $4.63$ ,  $p = 7.0 \times 10^{-6}$  and  $7.2 \times$   
 341  $10^{-4}$ , respectively.

#### 342 *Pattern classification*

343 *Item-level decoding.* In the *Occipital Sample* ROI the remembered direction of motion  
 344 could be successfully decoded from the delay period on a time point-by-time point basis for the  
 345 1M condition, and from the delay period of all three conditions when signal was collapsed across  
 346 all delay time points (10-14 sec, all  $ps < 0.05$ ; Figure 2C). Comparison between conditions  
 347 indicated that delay-period decoding performance was significantly superior for the 1M  
 348 condition relative to 3M and 1M2C ( $t(11) = 4.19$ ,  $p = 0.005$ ;  $t(11) = 3.84$ ,  $p = 0.008$ ,  
 349 respectively), but that it didn't differ between 3M and 1M2C ( $t(11) = 1.00$ ,  $p > 0.999$ ).

350 In contrast to the *Occipital Sample* ROI, decoding performance in the *Parietal Delay* ROI  
 351 was much weaker and much more variable. Time point-by-time point classification was only  
 352 significant in early portions of the delay in the 1M condition. Likewise, difference between 1M  
 353 and 3M conditions was also observed only during the early delay period.

354 *Category-level decoding.* In both the *Occipital Sample* ROI and the *Parietal Delay* ROI,  
 355 MVPA successfully discriminated 1M from 3M from 1M2C trial types at  $ps < 0.001$  for all  
 356 pairwise comparisons.

#### 357 *Task-related patterns of covariation in BOLD activity, MVPA, and behavioral precision*

358 In the *Occipital Sample* ROI, and replicating a previous finding (Emrich et al., 2013),  
 359 ANCOVA of data from 1M and 3M revealed a significant within-subject correlation relating the

load-related decline in MVPA to the load-related decline in behavioral precision ( $r^2 = 0.33$ ,  $p = 0.038$ ; Figure 3A).

Next, and of primary theoretical interest for the present study, we carried out a series of ANCOVAs intended to elucidate functional correlates of the elevated delay-period activity in the *Parietal Delay* ROI. Beginning with the 1M vs. 3M comparison, a significant within-subject correlation indicated that the load-related increase in delay-period signal in the *Parietal Delay* ROI was negatively related to the load-related decrease in behavioral precision ( $r^2 = 0.59$ ,  $p = 0.002$ ; Figure 3B). Note that this is the opposite pattern from what was observed in the *Occipital Sample* ROI. Furthermore, a second ANCOVA indicated that the 1M-to-3M load-related increase in delay-period signal was also significantly negatively related to the load-related decrease in classification performance in the *Occipital Sample* ROI ( $r^2 = 0.68$ ,  $p = 0.00055$ ; Figure 3C). Interestingly, neither of these effects was significant in comparable analyses comparing the load manipulation of 1M vs. 1M2C ( $r^2 = 0.14$ ,  $p = 0.206$ ;  $r^2 = 0.09$ ,  $p = 0.312$ ).

#### *Anatomically defined ROIs*

Although our primary theoretical interest was in the functions of delay-period activity in the *Parietal Delay* ROI, the results from this ROI were necessarily biased by our voxel selection procedure. Therefore, to address more general questions about the organization VWM functions in posterior parietal cortex, we repeated all the aforementioned analyses in the anatomical ROIs covering the IPS. To anticipate our findings in summary, the results revealed a gradient along the IPS, with the delay-period signals and analytically derived effects in the caudal-most portions of IPS generally weak or not detectable, and progressively taking on the characteristics of the *Parietal Delay* ROI at progressively more rostral subregions along the IPS.

382 *Group-average effects.* Beginning with delay-period BOLD activity, inspection of the  
 383 time series data revealed that it decreased to baseline by the end of the delay in IPS0, but became  
 384 progressively more elevated with more rostrally located ROI (not shown). An F test of parameter  
 385 estimates from GLM delay covariates, collapsing across 1M, 3M, and 1M2C conditions,  
 386 indicated a highly significant caudal-to-rostral increase ( $F(5,66) = 19.08$ ,  $p = 1.1 \times 10^{-11}$ ; Figure  
 387 4A). Similarly, the 1M vs. 3M effect of load also increased progressively from IPS0 to IPS5  
 388 ( $F(5,66) = 3.11$ ,  $p = 0.014$ ; Figure 4B).

389 An F test of average delay-period MVPA performance failed to find evidence for a  
 390 similar gradient ( $F(5,66) = 0.10$ ,  $p = 0.992$ ). We further examined the MVPA performance for  
 391 each condition separately, and performed *t* tests to evaluate the significance of classifier  
 392 performance in each subregion. Consistent with the results in the *Parietal Delay* ROI, only the  
 393 1M condition showed a trend of successful decoding of motion direction (Figure 3C; Also see  
 394 Table 2 for statistical results).

395 To better interpret the marginally significant decoding results in IPS, we calculated Bayes  
 396 factor for each of the comparisons. The Bayes factor analysis showed a gradient of the amount of  
 397 evidence in favor of the alternative hypothesis along IPS. For the 1M condition, the alternative  
 398 hypothesis (decoding performance higher than 0) was more likely than the null hypothesis  
 399 (decoding performance not different from 0) in caudal parts of IPS (IPS0-2) for the 1M  
 400 condition, and vice versa in IPS3-5. For the 3M and 1M2C conditions, in contrast, the Bayes  
 401 factors in all parietal ROIs (with the exception of IPS5 in the 1M2C condition) revealed greater  
 402 evidence in the data for the null hypothesis (Table 2).

403 *Patterns of covariation.* Recall that, in the *Parietal Delay* ROI, the level of BOLD signal  
 404 in the 1M vs. the 3M condition predicted the effects of this manipulation on behavioral precision.

At a finer grain of anatomical resolution, this relation was not observed in IPS0 and IPS1 ( $r^2 = 0.028$  and  $0.10$ , respectively), began to emerge in IPS2 ( $r^2 = 0.31$ ), and was uniformly robust for IPS3-IPS5 ( $r^2s > 0.40$ ; Figure 5A). Recall as well that, in the *Parietal Delay* ROI, the level of BOLD signal in the 1M vs. the 3M condition also predicted the effects of this manipulation on MVPA performance in the *Occipital Sample* ROI. In the anatomically defined ROIs, this effect was not significant in IPS0 and IPS1 ( $r^2 = 0.0004$  and  $0.21$ , respectively), but was robust and progressively stronger from IPS2-IPS5 ( $r^2s > 0.40$ ; Figure 5B).

#### *Exploratory analyses by hemisphere, and of lateral prefrontal cortex*

All of the analyses of IPS ROIs that have been reported up to this point suggest a much more prominent role for IPS activity, whether assessed as aggregated BOLD signal intensity or with MVPA, in the delay-period control of working memory for three items drawn from the same category than for three items drawn from two different stimulus categories. Furthermore, BOLD signal intensity of IPS delay-period activity was comparable in the 1M and 1M2C conditions, and the 1M to 1M2C load effect in IPS failed to show within-subject correlation with either neural or behavioral precision. Although these findings provided clear answers to the two principal questions that motivated this experiment, they left unanswered how our data might explain the general effects of memory load: the fact that behavioral precision was comparably lower for both 3M and 1M2C trials relative to 1M; and the fact that delay-period stimulus decoding from occipital cortex was comparably lower for both 3M and 1M2C trials relative to 1M. To address this question, we returned to the theoretical proposition that an amodal attentional resource underlies VWM capacity limitations. Because previous studies carried out within this framework have primarily identified load-sensitive modality-independent effects in left-hemisphere regions of IPS and frontal cortex (Cowan et al., 2011; Li et al., 2014; Majerus et

al., 2016), we carried out these additional analyses in the left-hemisphere and right-hemisphere  
*Parietal Delay* ROIs, and in the left-hemisphere and right-hemisphere *Lateral PFC Delay* ROIs  
 (as described in *Materials and Methods*).

In a unilateral left-hemisphere *Parietal Delay* ROI, 1M2C delay-period activity  
 (averaged across 10-14 sec) was significantly higher than was 1M delay-period activity ( $t(11) =$   
 $2.28, p = 0.043$ ), and the ANCOVA relating load-related change in delay-period activity to  
 behavioral precision also approached significance ( $r^2 = 0.24; p = 0.09$ ); no such trends were in  
 evidence in the right hemisphere. Importantly, in the left-hemisphere *Lateral PFC Delay* ROI,  
 delay-period activity was elevated for both the 1M2C and 3M conditions relative to 1M, and did  
 not differ between 1M2C and 3M (Figure 6A). Furthermore, for both of these conditions, the  
 ANCOVAs relating BOLD signal intensity in the left-hemisphere *Lateral PFC Delay* ROI to  
 behavioral precision and to occipital MVPA, as a function of memory load, revealed reliable  
 within-subject correlations ( $r^2s > 0.3; ps < 0.05$ ; Figure 6C-F); such trends became a lot weaker  
 in the right-hemisphere *Lateral PFC Delay* ( $r^2s = 0.29$  and  $0.03, ps = 0.06$  and  $0.55$ ), where  
 delay-period activity for the 1M2C condition was reduced (Figure 6B).

#### Discussion

Although delay-period activity in the IPS increases monotonically with memory load  
 (Emrich et al., 2013), and in a manner that saturates with VWM capacity (Todd and Marois,  
 2004, 2005), the functions that this activity supports remain unclear. Many studies to date have  
 confounded memory load with the potential for elevated demands on context binding. It is well  
 established, both at behavioral (Wickens et al., 1963; Wickens, 1973) and neural (Postle et al.,  
 2004; Cohen et al., 2014) levels, that mnemonic representations of same-category items interfere

451 to a greater extent than heterogeneous items. Furthermore, our serial presentation and single-item  
 452 probing procedure required subjects to retain not just the physical properties of each stimulus,  
 453 but also the order in which it had been presented. 3M trials were expected to place greater  
 454 demands on context binding (Oberauer and Lin, 2016), for the reason that the ordinal context of  
 455 each item could be confused with those of two other items, whereas on 1M2C trials such  
 456 confusion was only possible for the two colors, but not for the single RDK. Despite these  
 457 considerations, however, the fact that VWM for heterogeneous items is also capacity limited left  
 458 open at least two possibilities for our study. First, neural operations recruited by 3M and 1M2C  
 459 may have differed only quantitatively, in which case capacity limitations in VWM might be  
 460 understood as deriving from limitations inherent in the operations summarized here. Second, and  
 461 more consistent with our findings, 3M and 1M2C trials may differentially tap into two discrete  
 462 sets of mental operations, one engaged to address demands of context binding, and one more  
 463 generally associated with capacity limitations, regardless of stimulus category or modality.  
 464 (Additionally, and mutually compatible with the context-binding account, the two load-of-three-  
 465 items conditions also afforded different strategies for chunking by category, a possibility that  
 466 cannot be disambiguated with the present design.)

467 *IPS and the control of demands on context binding*

468 Delay-period activity in IPS was much more strongly implicated in controlling the effects  
 469 of stimulus homogeneity than in the effects of varying memory load. Spatially aggregated delay-  
 470 period BOLD activity was greater for 3M than for 1M and 1M2C, and did not differ between the  
 471 latter two. Furthermore, IPS BOLD sensitivity to the 1M-to-3M manipulation predicted the 1M-  
 472 to-3M drop in VWM fidelity, both as estimated in behavioral performance and in delay-period  
 473 decoding of occipital stimulus representation. No such relations were observed in 1M vs. 1M2C

474 comparisons. This means that factors other than load, per se, drove these within-subject  
 475 correlations. Although our results do suggest a possible alternative explanation for the load-  
 476 sensitive activity reported in the earlier work by Todd and Marois (2004; 2005), our study used a  
 477 different method to define the functionally activated ROI. Therefore, we cannot rule out the  
 478 possibility that there are two discrete sources of load-sensitive activity, one putatively related to  
 479 context binding, the other to memory storage.

480 Our findings are broadly consistent with the operation of a salience map (Colby and  
 481 Goldberg, 1999; Knops et al., 2014) under conditions in which the most behaviorally relevant  
 482 stimulus dimension to be tracked is order of presentation, rather than the more traditionally  
 483 studied spatial location (Jerde et al., 2012). The representation of temporal order information  
 484 engages PPC and lateral PFC (Marshuetz et al., 2000). Interestingly, many current computational  
 485 models also emphasize that context binding is fundamental to VWM function, and that the  
 486 critical context can often be temporal (Oberauer and Lin, 2016; Schneegans and Bays, 2017).  
 487 Because only temporal order served as context in the present study, it remains to be examined  
 488 whether this “context binding” hypothesis generalizes to other domains, such as space.

489 Despite the marked differences of processing requirements between the 3M and 1M2C  
 490 conditions, data from these two conditions were also similar in many respects. Behaviorally, the  
 491 two conditions did not differ statistically in terms of precision, probability of target responses, or  
 492 guessing. Neurally, decoding of the critical motion direction from the *Occipital Sample* ROI did  
 493 not differ between these two. Furthermore, swap errors for RDK stimuli, which were only  
 494 possible in the 3M condition, were nonexistent. The most parsimonious explanation for these  
 495 outcomes is that the additional demands of the 3M condition, relative to 1M2C, were overcome  
 496 by the recruitment of IPS-based control. The absence of swap errors may be explained by the



497 effective implementation of context binding, which is reflected in the greater delay-period  
 498 activity in IPS in the 3M condition.

499 *Constraints on working memory capacity*

500       The patterns of IPS activity that we have emphasized up to this point have not shown  
 501 strong evidence for activity related to category-independent capacity limitations on VWM. One  
 502 would expect a region whose activity reflected more general capacity limitations to show greater  
 503 delay-period activity for 1M2C than 1M. Consistent with previous studies (Cowan et al., 2011;  
 504 Li et al., 2014; Majerus et al., 2016), our data suggests that such activity is strongly left  
 505 lateralized, trending in IPS, and robust in lateral PFC. Indeed, our data are consistent with a  
 506 model of at least partial independence between a left-lateralized amodal attentional resource that  
 507 most prominently draws on lateral PFC (Cowan, 1995), and an IPS-supported salience map that  
 508 can carry out the function of context binding. This pattern is also consistent with computational  
 509 models that posit distinct explanations for binding errors versus the effects of load, the latter  
 510 being attributed to changes in signal-to-noise (Oberauer and Lin, 2016; Schneegans and Bays,  
 511 2017), as would be expected in a system operating under a normalization regime (Carandini and  
 512 Heeger, 2012).

513 *Functional distinction between occipital and parietal cortex, and a gradient of function along the*  
 514 *IPS*

515       Together with evidence for the dissociability of two kinds of control, our data also  
 516 confirmed a clear distinction between patterns of activity in occipital cortex versus IPS,  
 517 suggesting different contributions to VWM. This dissociation is highly robust and replicable, in  
 518 that three previous studies (Emrich et al., 2013; LaRocque et al., 2017; Riggall and Postle, 2012)  
 519 have demonstrated similar patterns of results. Whereas aggregated delay-period BOLD signal

intensity in the *Occipital Sample* ROI did not differ between the three conditions, nor from baseline levels; in the *Parietal Delay* ROI it was elevated in all three conditions, and markedly more so for 3M than 1M2C and 1M. This IPS activity is associated with a control function, as it's correlated with both behavioral and neural estimates of VWM fidelity. In contrast, delay-period MVPA decoding, which suggests a role in information storage, was markedly superior in the *Occipital Sample* ROI. Specifically, decoding of mnemonic representations was successful in the *Occipital Sample* ROI regardless of memory load, whereas successful decoding in the parietal ROIs was only possible, or trending, when only one item was held in memory.

The contribution of the parietal cortex to VWM storage, per se, is controversial and remains to be fully understood. Task-specific delay-period selectivity for motion direction was not observed in single neurons in the lateral intraparietal area (LIP) of monkeys (Sarma et al., 2016). However, delay-period motion direction can be decoded from local field potentials regardless of task (Masse et al., 2017). Another study has demonstrated that LIP neurons encode the magnitude of the difference in shape between a target and a nonmatching foil rather than shape identity (Ong et al., 2017). Human fMRI studies also produced mixed findings, with some successful (Christophel et al., 2012; Ester et al., 2015; Bettencourt and Xu, 2016; Yu and Shim, 2017) and some unsuccessful (Linden et al., 2012; Riggall and Postle, 2012; Emrich et al., 2013; Lee et al., 2013) when decoding stimulus identity from delay-period activity in the parietal cortex.

Along the length of the IPS, differences in function were graded, rather than categorical. 1M-to-3M load sensitivity of delay-period activity was lowest for IPS0 and became progressively greater for each more rostrally located ROI. This gradient was mirrored in the results of analyses indexing control-related patterns of activity: The evidence for functional

543 interactions between parietal signals and occipital mnemonic representations, as well as the  
544 evidence for a relation between parietal signals and behavior, were non-existent for the more  
545 caudal part of IPS and became progressively larger for more rostral parts. Thus, rather than being  
546 highly localized, the working-memory-related control functions of the IPS may emerge and  
547 strengthen along a caudal-to-rostral gradient. This observation is broadly consistent with  
548 longstanding views suggesting a functional distinction between caudal and rostral IPS (Cole et  
549 al., 2013; Freud et al., 2016; Xu and Chun, 2006).

550 *The neural bases of working memory capacity limitations*

551 Empirical observation has demonstrated that VWM is capacity limited (Luck and Vogel,  
552 1997; Cowan, 2001), with individual differences stable and trait-like (Fukuda et al., 2015), and  
553 predictive of many other cognitive measures (Cowan, 2014). Although this characteristic of  
554 human cognition undoubtedly derives from many sources, two that have received considerable  
555 attention are an amodal resource that must be allocated across all to-be-held items in memory,  
556 and processes to control interactions among mnemonic representations. Our results provide  
557 evidence that these two are mutually compatible, and supported by at least partially dissociable  
558 systems in the brain.

559

**Table 1.** Behavioral responses to direction-of-motion probes

Trial type	Descriptive data		2-factor mixture model (parameter estimates)			
	Distribution of response error (converted to 1/SD)	RT (sec)	Probability of response to target	Probability of response to non-target	Probability of guess response	Concentration
1M	2.97 [0.47]	2.42 [0.47]	0.932 [0.26]	n/a	0.068 [0.003]	30.2 [0.47]
3M	1.84 [0.31]	2.66 [0.09]	0.867 [0.40]	0.002 [0.002]	0.131 [0.039]	20.1 [3.1]
1M2C	2.36 [0.37]	2.55 [0.09]	0.901 [0.41]	n/a	0.098 [0.004]	20.4 [2.5]

All values in brackets are standard error of the mean; n/a = not applicable

563 **Table 2.** Statistical results of MVPA performance for 1M, 3M, and 1M2C conditions separately

	<i>t</i> value			<i>p</i> value (FDR corrected in each condition, for anatomically-defined ROIs)			Bayes factor		
	1M	3M	1M2C	1M	3M	1M2C	1M	3M	1M2C
<i>Parietal Delay ROI</i>	1.83	0.58	1.58	0.094	0.576	0.142	0.57	0.02	0.25
IPS0	2.37	0.32	0.92	0.075	0.752	0.378	2.64	0.75	0.10
IPS1	2.45	0.48	1.94	0.075	0.752	0.122	2.23	0.02	0.47
IPS2	2.57	0.65	1.75	0.075	0.752	0.131	4.29	0.02	0.01
IPS3	1.91	0.79	1.92	0.100	0.752	0.122	0.65	0.02	0.66
IPS4	2.05	0.82	2.01	0.098	0.752	0.122	0.80	0.02	0.74
IPS5	0.93	0.84	2.18	0.370	0.752	0.122	0.11	0.02	1.03

564

565

566 **Figure 1.** Experimental procedure.

567 Participants fixated at the center of the screen and remembered one motion direction (1M), one  
568 motion direction and two colors (1M2C), or three motion directions (3M) on different trials.  
569 After a long delay of 8 s, participants rotated the needle to indicate the probed motion direction  
570 or color.

571

572 **Figure 2.** BOLD activity and classification performance in Sample and Delay ROIs

573 *A.* Time course of BOLD activity in *Occipital Sample* ROI, and *B.* in *Parietal Delay* ROI. *C.*  
574 Time course of classifier performance in *Occipital sample* ROI, and *D.* in *Parietal Delay* ROI.  
575 Red, blue, and green lines represent the 1M, 3M, and 1M2C conditions, respectively. Circles on  
576 top of each plot denote significance of each time point. Purple, Orange, and Cyan circles  
577 represented the comparisons of 1M vs. 3M, 1M vs. 1M2C, and 3M vs. 1M2C, respectively. Solid  
578 circles:  $p < 0.05$ ; dashed circles:  $p < 0.10$ . All  $p$ -values were corrected with False Discovery Rate  
579 (FDR). The shaded gray areas indicate the timing of the sample (S), delay (D), and probe (P)  
580 epochs of each trial. Error bars denote  $\pm 1$  SEM.

581

582 **Figure 3.** Within-subject correlations between behavioral precision, BOLD activity, and  
583 classification sensitivity, as a function of memory load (1M vs. 3M).

584 *A.* Results from ANCOVA relating behavioral precision (concentration parameter from mixture  
585 model) and classification performance in *Occipital sample* ROI. *B.* Results from ANCOVA  
586 relating behavioral precision and delay-period BOLD activity (beta value from GLM) in *Parietal*  
587 *Delay* ROI. *C.* Results from ANCOVA relating delay-period BOLD activity in *Parietal Delay*  
588 ROI and classification sensitivity in *Occipital sample* ROI. In each plot, data from each subject

are portrayed in a different color, and the “1” and “3” symbols display individual values in the 1M and 3M conditions, respectively. Lines illustrate the best fit of the group-level linear trend (i.e., the within-subject correlation) in relation to each individual subject’s data.

**Figure 4.** Delay-period BOLD activity and classification sensitivity in each IPS anatomical ROI. **A.** Delay-period BOLD activity, collapsing across 1M, 3M, and 1M2C conditions. **B.** Load effect [3M – 1M]. **C.** Mean classification of averaged delay-period signal for the 1M condition in the functionally defined *Occipital sample* and *Parietal Delay* ROIs, and in anatomically defined IPS0-IPS5. Error bars denote  $\pm 1$  SEM.

**Figure 5.** Within-subject correlation between behavioral precision, BOLD activity, and classification sensitivity, as a function of memory load (1M vs. 3M), in each IPS anatomical ROI. **A.** Results from ANCOVAs relating behavioral precision and BOLD activity. **B.** Results from ANCOVAs relating BOLD activity in each IPS anatomical ROI and classification performance in the *Occipital sample* ROI.

**Figure 6.** BOLD activity and within-subject correlation in the Lateral PFC ROIs. **A.** Time course of BOLD activity in left hemisphere Lateral PFC ROI, and **B.** right hemisphere Lateral PFC ROI. Red, blue, and green lines represent the 1M, 3M, and 1M2C conditions, respectively. Circles on top of each plot denote significance of each time point for 1M vs. 3M (purple), 1M vs. 1M2C (orange), and 1M2C vs. 3M (cyan). Solid circles:  $p < 0.05$ ; dashed circles:  $p < 0.10$ . The shaded gray areas indicate the timing of the sample (S), delay (D), and

612 probe (P) epochs of each trial. Error bars denote  $\pm 1$  SEM. **C.** Results from ANCOVAs relating  
613 variation as a function of the 1M vs. 3M manipulation between BOLD activity in the left  
614 hemisphere Lateral Prefrontal ROI and behavioral precision, and **D.** between BOLD activity in  
615 the left hemisphere Lateral Prefrontal ROI and classifier performance from *Occipital sample*  
616 ROI. **E.** Results from ANCOVAs relating variation as a function of the 1M vs. 1M2C  
617 manipulation between BOLD activity in the left hemisphere Lateral Prefrontal ROI and  
618 behavioral precision, and **F.** between BOLD activity in the left hemisphere Lateral Prefrontal  
619 ROI and classifier performance from *Occipital sample* ROI. In each plot, data from each subject  
620 are portrayed in a different color, and the “1”, “2”, and “3” symbols display individual values in  
621 the 1M, 1M2C, and 3M conditions, respectively.



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