

Complementary univariate and multivariate signals in the parietal cortex for visual working memory pointers and features

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An emerging body of work in visual working memory (VWM) has embraced the theoretical construct of pointers: an object is mentally represented by a content-free pointer binding the corresponding features together. In the current magnetoencephalography (MEG) study, we investigated univariate and multivariate neural responses modulated by number of objects and by number/content of features in two literature-driven posterior parietal patches: inferior and superior intraparietal sulcus (IPS). We found that, across VWM formation and maintenance, number of objects (or attended locations) is tracked by univariate signals in the inferior IPS, but by multivariate signals in the superior IPS. Feature information manifests in multivariate signals in both superior and inferior IPS across VWM formation and maintenance, and additionally in univariate signals in the inferior IPS during VWM formation. Taken together, our results suggest that complementary univariate and multivariate neural responses underlie VWM in the posterior parietal cortex.

Keywords visual working memory (VWM), pointer, MEG (magnetoencephalography), posterior parietal cortex, multivariate analysis

Introduction

Human visual working memory (VWM), or visual short-term memory, enables us to hold multiple items temporarily, in service of future tasks or computations. This capacity-limited cognitive faculty, remarkably, underlies our extremely flexible cognition and behavior (Ballard et al. 1997; Xie et al. 2020; Van Ede and Nobre 2023; Wyble et al. 2025). While it is clear that we can hold multiple (up to 3 or 4) visual objects in VWM (Cowan 2001; Awh et al. 2007; Zhang and Luck 2008; Adam et al. 2017), the format—or data structure—of such representation, and how the brain supports this data structure remain a topic of ongoing debate.

One influential proposal is that an object is registered in VWM by a pointer (Bowman and Wyble 2007; Swan and Wyble 2014; Balaban et al. 2019; Yu and Lau 2023; Ngiam 2024; Awh and Vogel 2025; Balaban and Luria 2025; Park 2025). These pointers, akin to pointers in programming languages, do not represent features of this object in themselves (Green and Quilty-Dunn 2021; Yu 2025). Rather, a pointer “points” to the representation of corresponding features; the pointers themselves are therefore “content-free” (Thyer et al. 2022; Jones et al. 2024a; Jones et al. 2024b; Yu and Lau 2025c). While this proposal was originally conceived as an algorithmic-level theory (Kahneman et al. 1992; Pylyshyn 2001), recent decades have seen a growing body of literature investigating how the brain implements these “pointers.”

Two major accounts of pointers or indexes differ in how they treat location information. One view holds that location is an integral and necessary part of pointer representations (Brody and Csibra 2026;

Turan-Küçük and Kibbe 2026), while the other view argues that pointers are separable from locations, with location serving as a bindable feature rather than a constitutive component (Jones et al. 2024a; Balaban 2026). We note at the outset that the current study is not designed to adjudicate between these accounts; in our design, the number of attended objects covaries with the number of attended locations. Indeed, we believe that spatial attention could be integral to setting up and maintaining pointers in VWM, rather than being understood as a confound (Xu and Chun 2009; for more detailed discussion see section Limitations and future directions). We therefore use the term “pointer” here to refer neutrally to representations of objects or objects + locations, without making commitments about the division between working memory and attention.

One puzzle in the existing neurocognitive research on VWM pointers is whether pointers are reflected by univariate or multivariate signals or both (Naughtin et al. 2016; Adam et al. 2025; Yu 2025). One region that has been spotlighted for pointers and VWM in general is the posterior parietal cortex (Berryhill 2012; Riggall and Postle 2012; Xu 2018). On the one hand, a line of functional magnetic resonance imaging (fMRI) studies reported that univariate signals in the posterior parietal patch of inferior intraparietal sulcus (inferior IPS) track the number of pointers (Xu and Chun 2006; Xu 2009; Naughtin et al. 2016; Bettencourt and Xu 2016a). These univariate signals increase as the number of objects increase, plateauing beyond 3 to 4 objects—the canonical capacity of VWM. Critically, as these signals seem not to be affected by the number or type of features (Xu and Chun 2006; Naughtin et al. 2016), they can be taken to reflect the number of

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pointers. On the other hand, a line of electroencephalography (EEG) studies investigated multivariate signals distributed across scalp sensors (Adam et al. 2020; Thyer et al. 2022). These multivariate signals track the number of pointers when the number or type of features are controlled for (Jones et al. 2024a; Jones et al. 2024b; Suplica et al. 2025).

Regarding the neural responses for feature information within the posterior parietal cortex, fMRI studies have revealed that multivariate signals in the superior IPS reflect feature content (Bettencourt and Xu 2016b; Vaziri-Pashkam and Xu 2017; Xu and Vaziri-Pashkam 2019). For example, multivariate signals in the superior IPS track object categories such as faces vs. houses (Xu and Vaziri-Pashkam 2019). Here, we use “feature content” to refer broadly to for example different values of the same type of feature (eg different orientations for gratings), and different types of lower- to higher-level features (eg orientation vs. color; different object categories); “feature information” includes both feature content and the number of features (eg the number of colors to be encoded). Additionally, univariate signals in the superior IPS have been found to reflect the number of features (Xu and Chun 2006; Xu 2009). For example, with the number of objects controlled for, univariate signals in the superior IPS are higher for more complex objects compared to less complex ones (Xu and Chun 2006).

Taken together, existing literature leaves open an intriguing possibility for a potential labor division across the inferior IPS and superior IPS for VWM, while where exactly the line is drawn remains to be fully delineated. Is this labor division primarily defined by pointers vs. feature information? Is this labor division primarily defined by the type of neural signals (univariate vs. multivariate)? How does this labor division unfold dynamically across different phases of VWM formation and maintenance?

Addressing these questions integratively requires a neuroimaging method with high spatiotemporal resolution. As fMRI offers excellent spatial resolution but is sluggish in time, and EEG offers excellent temporal resolution but suffers from suboptimal spatial resolution, to fully examine univariate vs. multivariate responses in inferior vs. superior IPS and across VWM formation vs. maintenance, we took advantage of magnetoencephalography (MEG)—a neuroimaging method with both acceptable spatial and temporal resolutions. The current study thus bridges two lines of work—providing spatiotemporally-resolved evidence from IPS on VWM (following earlier work with fMRI, Xu and Chun 2009), while situating the findings within the emerging framework of VWM pointers.

To this end, we employed a design that manipulated object load (ie the number of pointers) and feature information orthogonally, in order to test the spatiotemporal dynamics of their corresponding neural responses in the superior and inferior IPS. We employed a 2×3 design, with 2 object load conditions (2 vs. 4 objects), and 3 feature conditions (color-only, orientation-only, and bifeatural [both color and orientation]; Fig. 1b), similar to Thyer et al. (2022). In color trials and orientation trials, only color or orientation needs to be encoded for each object, while in bifeatural trials, both color and orientation need to be encoded for each object.

Materials and methods

Data and processing scripts for this study are openly shared on OSF (Open Science Framework; <https://osf.io/jwumn/>).

Participants

A total of 27 participants (age 19 to 26, 14 female) entered our data analysis. One additional participant was excluded because of

chance-level (49%) performance in some blocks. Informed consent was obtained from all participants and they received monetary reimbursement or course credit for their participation. The procedures were approved by the Institutional Review Board of University of Maryland College Park (Protocol #: 371754).

Procedure

Each participant was presented with 600 trials: 200 color trials, 200 orientation trials, and 200 bifeatural trials. Within each feature condition (color, orientation, bifeatural), half of the trials had a load of 2 objects and half had a load of 4 objects. These 600 trials were evenly divided into 6 blocks: 2 color blocks, 2 orientation blocks, and 2 bifeatural blocks. Each block contained 100 trials, and the order of the blocks was randomized for each participant, with the constraint that each type of block appeared once in the first 3 and last 3 blocks, respectively. In other words, the trials in each block belonged to the same feature condition (color, orientation, bifeatural) but were intermixed in terms of memory load (2 vs. 4 objects).

In each trial, the participants were first presented with a fixation cross with a duration of 800 ms against a gray background, followed by a sample memory array with a duration of 250 ms (see Fig. 1c). The sample consisted of 2 or 4 unique target objects. For the color trials, the colors were sampled without replacement from the following 7 colors: red [255,0,0], green [0,255,0], blue [0,0,255], yellow [255,255,0], purple [255,0,255], teal [0,255,255], and orange [255,128,0]. For the orientation trials, the bar orientation was sampled without replacement from the following 4 orientations: 0°, 45°, 90°, and 135°. The color of the disk behind these target orientations was randomly sampled from the above colors for each participant and was kept consistent throughout that experimental session for that participant. For bifeatural trials, each target object was a combination of a color and an orientation sampled in the aforementioned way. The target objects ($2.1^\circ \times 2.1^\circ$) occupied 2 or 4 out of all 8 boxes (light gray [191,191,191], $2.5^\circ \times 2.5^\circ$ each), located at 8 fixed locations evenly distributed 4.5° from the center of the screen. The box contours were employed to discourage grouping (Xie and Zhang 2017). Filler gray disks ([166,166,166]) occupied the rest of the locations for all trials, additionally with orientation bars at a random orientation for the orientation and bifeatural trials. The orientation bars had a width of 0.5° . A blank screen delay of 1,000 ms followed the sample, after which the probe appeared on the screen.

For the probe, only 1 object was presented at one of the locations previously occupied by a target object. Half of the trials had a match probe, and the other half had a change probe. On “match” trials, this object was the same one as the one in the sample for that location; on “change” trials, this probe object was randomly selected from other target features used in this trial. For example, for a change trial in the color condition, participants were probed with a color that appeared in the sample but not at the probed location. For a change trial in the bifeatural condition, participants were probed with an object with the right color for that location but a wrong—yet previously presented—orientation (or the right orientation yet a wrong color). This setup required the participants to represent bindings across features instead of free-floating features (Yu and Lau 2025a), as feature binding is hypothesized to be one of the key functions of pointers (see Yu and Lau 2023 for review). Participants pressed one button to indicate “match,” and pressed another button to indicate “change” (buttons randomized for each participant), with no time limit for response. After their response, they were shown a line of asterisks on the screen,



Figure 1 a) Illustration of the superior IPS and inferior IPS ROIs. b) Experimental conditions: we employed a 2×3 design, with 2 object load conditions (2 vs. 4 objects), and 3 feature conditions (color-only, orientation-only, and bifeatural). c) Illustration of a trial across 3 feature conditions with the example of object load = 4.

where they would press any button to proceed to the next trial in a self-paced manner. Prior to the experiment, participants were instructed to blink only during this period, and to avoid blinking during the trials. While the fixation cross was presented on the screen, the participants were instructed to fixate on it. They were also instructed against verbal rehearsal. At least 24 practice trials were run for each participant prior to the experiment. The setup was broadly consistent with the EEG study of [Thyer et al. \(2022\)](#), and the experiment was run in MATLAB R2009a with Psychtoolbox 3 ([Brainard 1997](#); [Kleiner et al. 2007](#)).

Behavioral analyses

Accuracy was calculated for each participant for each condition. The responses were subjected to a 2×3 repeated-measures analysis of variance (ANOVA) (object load: 2, 4 $\times$ feature: color, orientation, bifeatural; [Fig. 1b](#)). Significant interactions were followed up with uncorrected pairwise comparisons using *t*-tests (2-tailed).

MEG recording

Prior to recording, 5 head position indicator coils were affixed to each participant's head, and the position of these coils relative to the nasion and tragus, as well as the participant's head-shape, were digitized using a Polhemus 3SPACE FASTRAK system in order to determine the participant's accurate placement in the MEG dewar. During the experimental sessions, participants lay supine in a dimly lit magnetically shielded room (Vacuumschmelze GmbH & Co. KG, Hanau, Germany). Continuous MEG recording was executed using a 160-channel axial gradiometer whole-head system (Kanazawa Institute of Technology, Kanazawa, Japan), and data were sampled at 1,000 Hz (60 Hz online notch filter, DC-200 Hz recording bandwidth).

MEG analyses

Sensor-level analyses

MEG sensor-level data were analyzed by customized code in MATLAB R2020b with MNE-Python 1.5.1 ([Gramfort et al. 2013](#)), with a similar procedure as [Yu and Lau \(2025a\)](#). First, noisy and flat channels were identified for each participant with Maxwell filtering, and

these channels (1 to 3 per participant) were interpolated with the MNE algorithm. Then the environmental magnetic interferences were suppressed using temporal signal space separation (tSSS; [Taulu and Simola 2006](#)). A low-pass infinite impulse response (IIR) filter with an upper cutoff frequency of 40 Hz was then applied to the MEG data. Ocular and cardiac artifacts were removed using independent component analysis (ICA; fastica algorithm); 2 to 7 ICA components were removed for each participant. Epochs of $-200:1,200$ ms time-locked to the presentation of sample stimuli in each trial were extracted. The 200 ms pre-stimulus interval was used as the baseline interval. Trials with a maximum peak-to-peak signal amplitude higher than 3,000 fT were excluded. For each participant, the number of epochs per condition was matched with the constraint of minimizing timing differences, using the mintime algorithm. This resulted in 88 to 100 epochs/condition entering further data analysis for each participant (that is, 88% to 100% of all trials, mean = 98.81%). For each participant and each condition (ie a certain load condition in a certain feature block), we calculated the mean event-related field (ERF) response for each channel. Following [Yu and Lau \(2025a\)](#), the right posterior activity (RPA) region of interest (ROI) was defined with the following channels: MEG054, MEG055, and MEG071. Mean ERFs were calculated within this ROI. Comparisons across conditions were statistically evaluated with repeated-measures ANOVA in JASP 0.18.1 ([JASP Team 2023](#)).

Source space analyses

For the source space analyses, the “fsaverage” template brain from the FreeSurfer software package (<http://surfer.nmr.mgh.harvard.edu>) was used as an approximation for individual anatomy (4-fold icosahedral subdivision), and digitizer data was used to manually coregister individual head position to the template brain. A 3-compartment boundary element model computed for this template brain with the linear collocation approach was used in the forward calculation ([Hämäläinen and Sarvas 1989](#); [Mosher et al. 1999](#)). Then we created an inverse operator for the averaged responses for each participant-condition combination. Noise covariance estimates were derived from data recorded in the $-200:0$ ms baseline period. The orientation of the dipoles was subjected to a loose constraint with weighting factor 0.2 ([Lin et al. 2006](#)), and depth was weighted at

0.8. Then the inverse operator was applied to the averaged evoked responses for the corresponding participant and condition, with regularization $\lambda = 1/9$ and the dynamic statistical parameter mapping (dSPM) algorithm (Dale et al. 2000). Individual estimates were then smoothed using 7 iterative steps to spread estimated activity to neighboring vertices.

The source space ROIs were defined a priori based on the fMRI study of Xu and Chun (2006), converting their original Talairach coordinates to MNI coordinates (Papademetris et al. 2006): inferior IPS, left [−25, −74, 30], right [25, −69, 36]; superior IPS, left [−14, −73, 51], right [15, −72, 55]. Each ROI was grown from the nearest vertex to these MNI coordinates, within a maximum radius of 10 mm on the white matter surface based on geodesic distance, constrained to the corresponding hemisphere. For each participant, the responses in each vertex in each ROI were averaged across all trials in the same condition for 2 time windows respectively: 200 to 400 ms (VWM formation) and 400 to 1,200 ms (VWM maintenance).

Univariate analysis

The responses for all vertices for each ROI were averaged, and were subjected to a 2×3 repeated-measures ANOVA (object load: 2, 4 $\times$ feature: color, orientation, bifeatural). Post hoc comparisons (2-tailed) across conditions were run with Bonferroni corrections within each ANOVA. For visual examination, a contrast map based on t -values was created by comparing across load conditions (paired t -test, 2-tailed) vertex by vertex with a threshold of $\alpha = 0.05$ across a series of 200 ms time windows from 200 to 1,200 ms (Fig. S1).

Multivariate analysis: object load and feature

For multivariate analysis, we took a representational similarity analysis (RSA) approach (Kriegeskorte et al. 2008; Jones et al. 2024a; Jones et al. 2024b; Suplica et al. 2025). For each participant, ROI, and time window, we calculated a neural similarity matrix based on the neural similarity characterized by Spearman's rank correlation for each pair of conditions. Here we utilized Spearman's rank correlation as it is immune to the absolute magnitude of responses, thus maximally detached from univariate signals. We then calculated a similarity matrix based on object load by calculating the reverse of the absolute difference. This similarity matrix was agnostic to feature information and only concerned the number of objects. For example, the “color, 2” condition (ie color, 2 objects) and “orientation, 4” condition (ie orientation, 4 objects) had an absolute difference of 2, because the former condition involved 2 objects and the latter one involved 4. As absolute difference increases as conditions are less similar, to calculate a similarity matrix, we took the opposite value of the absolute difference. The similarity matrix for feature was calculated similarly to the univariate analysis, that is, we considered “color,” “orientation,” and “bifeatural” as 3 separate feature conditions. The similarity between experimental conditions of the same feature condition was noted as 0, and the similarity between experimental conditions of different feature conditions was noted as −1.

Then for each participant, we conducted a multiple regression for each region-time window combination, with the neural similarity matrix as the dependent variable, and object load and feature similarity matrices as independent variables, rendering a beta value for object load and feature respectively. All variables were z-scored prior to regression. The beta values for all participants for each region-time window-factor combination were compared against 0 with a 1-sample t -test (2-tailed). The P -values were false discovery rate (FDR)-adjusted

with the Benjamini–Hochberg procedure (denoted as P_{FDR}) within each brain region (Benjamini and Hochberg 1995; Xu and Chun 2025; Groppe 2026). Variance inflation factors (VIFs) were calculated as the diagonal elements of the inverse of the correlation matrix (Belsley et al. 1980; Vasilaky 2016).

In the above analysis (Fig. 4), the similarity matrix for features assumed a tripartition across color, orientation, and bifeatural conditions. To gauge the robustness of this RSA analysis, we additionally carried out analyses with the same pipeline, but instead treating the similarity between single-feature and bifeatural conditions as 0.2, 0.5, 0.8, and 1 (Fig. S3). The results of assigning this value of 0.5—a value between 0 and 1—were visualized in Fig. 5a.

Multivariate analysis: object load, feature type, and feature count

The procedures were identical to the analysis in Fig. 5a, except for the following. We added a similarity matrix for the total feature count to the model (Fig. 5b). The feature count similarity matrix was created based on the reverse of the absolute difference for the total count of features. For example, the “color, 2” condition had a total feature count of 2, and the “bifeatural, 2” condition had a total feature count of 4, so the similarity between the 2 conditions was −2. The “color, 2” condition had a total feature count of 2, and the “bifeatural, 4” condition had a total feature count of 8, so the similarity between these 2 conditions was −6. In this case, conditions closer in feature count rendered a more positive similarity value.

Results

Behavioral results

For each of the 6 conditions, participants had above-chance performance, with bootstrapped 95% CIs as follows: color, 2 (93.1% to 96.0%), color, 4 (77.2% to 85.1%), orientation, 2 (83.9% to 89.7%), orientation, 4 (66.4% to 71.7%), bifeatural, 2 (84.6% to 89.1%), and bifeatural, 4 (64.9% to 69.6%). A 2 (object load: 2, 4) $\times$ 3 (feature: color, orientation, bifeatural) repeated-measures ANOVA revealed a significant main effect of object load, $F(1,26) = 403.28$, $P < 0.001$, $\eta_p^2 = 0.94$, a significant main effect of feature, $F(2,52) = 81.96$, $P < 0.001$, $\eta_p^2 = 0.76$, as well as a significant interaction effect, $F(2,52) = 5.37$, $P = 0.008$, $\eta_p^2 = 0.17$. The interaction effect appeared to be driven by a larger numerical impact of object load on orientation and bifeatural trials compared to the color trials: comparing the drop in accuracy across load 2 and 4 conditions, we observed a significant difference between color and orientation trials (paired t -test, 2-tailed, uncorrected, $t(26) = -2.13$, $P = 0.04$, Cohen's $d = -0.41$), and a significant difference between color and bifeatural trials ($t(26) = -2.98$, $P = 0.006$, Cohen's $d = -0.57$), but not a significant difference between orientation and bifeatural trials ($t(26) = -1.07$, $P = 0.30$, Cohen's $d = -0.21$). While the magnitude of the object load effect was thus greatest in orientation and bifeatural trials, color conditions still showed a robust, statistically significant load effect in their own right ($t(26) = 7.89$, $P < 0.001$, Cohen's $d = 1.52$).

MEG sensor-level results

Similar to our prior study (Yu and Lau 2025c), we analyzed the ERF responses in the 400 to 1,200 ms time window in right posterior sensors (the RPA ROI). A 2 (object load: 2, 4) $\times$ 3 (feature: color, orientation, bifeatural) repeated-measures ANOVA revealed a significant main effect of object load, $F(1,26) = 21.88$, $P < 0.001$, $\eta_p^2 = 0.46$, as well

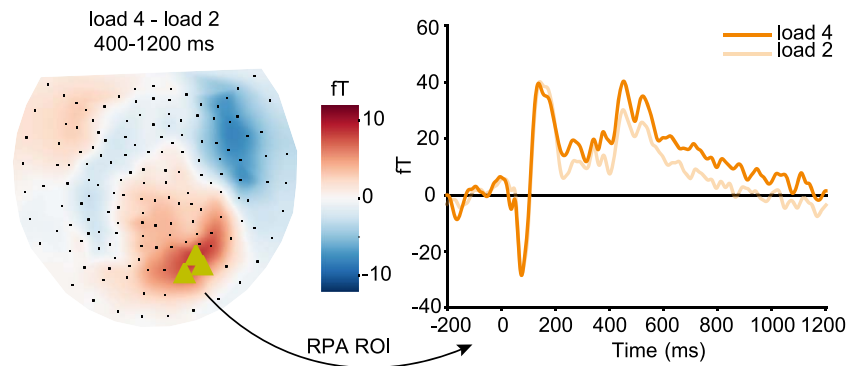


Figure 2 ERF responses at the RPA ROI across the 2 load conditions. ERF: event-related field; RPA: Right posterior activity; ROI: Region of interest. For ERFs of each of the 6 experimental conditions see Fig. S2 in supplementary materials.

as a significant interaction effect, $F(2,52)=4.39$, $P=0.02$, $\eta_p^2=0.14$. The main effect of feature was not statistically significant, $F(2,52)=1.51$, $P=0.23$, $\eta_p^2=0.06$ (see Fig. 2).

Follow-up paired t -tests across 2 object load conditions revealed a significant difference for color trials, $t(26)=-4.23$, $P<0.001$, Cohen's $d=-0.82$, as well as for the bifeature trials, $t(26)=-3.19$, $P=0.004$, Cohen's $d=-0.61$. The difference was only numerical for the orientation trials, $t(26)=-1.46$, $P=0.16$, Cohen's $d=-0.28$. These results are largely in line with prior reports that RPA is sensitive to the number of pointers but not the number of features (Yu and Lau 2025c).

We report sensor-level RPA results here following recent studies suggesting RPA as a candidate neural marker for VWM pointers (Yu and Lau 2025c), providing some continuity with the existing literature before we turn to our primary, source-level analyses. Such an interpretation of RPA is in line with our current results, except for the null load effect in orientation trials. However, as null results should be interpreted with care and the numerical difference is in the predicted direction, future studies are needed to fully evaluate the relationship between RPA and pointers. Because the focus of the present study is the source-level analyses, we do not discuss the sensor-level results further.

magnetoencephalography (MEG) source-level results

Univariate analysis

For inferior IPS, a main effect of object load emerged for VWM formation ($F(1,26)=4.13$, $P=0.05$, $\eta_p^2=0.14$), and extended into VWM maintenance ($F(1,26)=5.92$, $P=0.02$, $\eta_p^2=0.19$). In contrast, no effects of feature were observed in this region. For VWM formation, neither the main effect of feature nor the interaction effect was statistically significant: feature, $F(2,52)=0.60$, $P=0.55$, $\eta_p^2=0.02$; interaction effect, $F(2,52)=0.80$, $P=0.46$, $\eta_p^2=0.03$. During VWM maintenance, neither the main effect of feature nor the interaction effect was statistically significant: feature, $F(2,52)=0.66$, $P=0.52$, $\eta_p^2=0.03$; interaction effect, $F(2,52)=0.40$, $P=0.67$, $\eta_p^2=0.02$ (see Fig. 3).

For superior IPS, a main effect of feature manifested for VWM formation, $F(2,52)=3.60$, $P=0.03$, $\eta_p^2=0.12$. The main effect of object load was only marginally significant, $F(1,26)=3.61$, $P=0.07$, $\eta_p^2=0.12$, and the interaction effect was non-significant, $F(2,52)=0.09$, $P=0.91$, $\eta_p^2=0.004$. Post hoc pairwise comparison (Bonferroni-corrected) across the 3 feature conditions revealed a significant difference between color and bifeature conditions, $t(26)=-2.68$, $P=0.03$, Cohen's $d=-0.16$. The differences between the other 2 pairs of

feature conditions were not statistically significant. During VWM maintenance, none of the effects were statistically significant (F -values < 2.48 , P 's > 0.12).

Multivariate analysis

We first constructed experimental similarity matrices based on a similar logic as the ANOVA for our univariate analysis. That is, an object load similarity matrix and a feature similarity matrix. In the feature similarity matrix, we considered the "color," "orientation," and "bifeature" conditions as 3 separate conditions (see Materials and Methods), mirroring the tripartition of feature conditions in the univariate analyses. To maximally disentangle this analysis from the absolute activation magnitudes relevant to univariate responses, we quantified neural similarity with the Spearman's rank correlation that only cared about the rank orders in the data. Multiple regression was administered to evaluate the contributions of object load and feature similarity toward neural similarity, rendering a beta value (β) for the object and feature, respectively, for each participant (see Materials and Methods).

For superior IPS, betas for object load and features were significantly different from 0 for both VWM formation and maintenance: object load, VWM formation, $t(26)=2.93$, FDR-adjusted $P_{FDR}=0.007$, Cohen's $d=0.56$; object load, VWM maintenance, $t(26)=3.41$, $P_{FDR}=0.003$, Cohen's $d=0.66$; feature, VWM formation, $t(26)=5.37$, $P_{FDR}<0.001$, Cohen's $d=1.03$; feature, and VWM maintenance, $t(26)=5.04$, $P_{FDR}<0.001$, Cohen's $d=0.97$ (see Fig. 4).

For inferior IPS, betas for only feature were significantly different from 0: feature, VWM formation, $t(26)=4.86$, $P_{FDR}<0.001$, Cohen's $d=0.94$; and feature, VWM maintenance, $t(26)=3.04$, $P_{FDR}=0.011$, Cohen's $d=0.58$. Betas for object load did not reach statistical significance: object load, VWM formation, $t(26)=1.25$, $P_{FDR}=0.30$, Cohen's $d=0.24$; object load, VWM maintenance, $t(26)=0.97$, $P_{FDR}=0.34$, Cohen's $d=0.19$. The difference between feature and object load was confirmed with a main effect of factor with a 2×2 repeated-measures ANOVA (factor: object load, feature $\times$ time window: VWM formation, VWM maintenance), $F(1,26)=16.25$, $P<0.001$, $\eta_p^2=0.39$. The main effect of time window and the interaction effect did not reach statistical significance (P 's > 0.17). The results are summarized in Table 1.

Complementary multivariate analyses

The tripartition across the 3 feature conditions, while in line with the structure of our univariate analysis, might assume a similarity structure where bifeature conditions are different from single feature

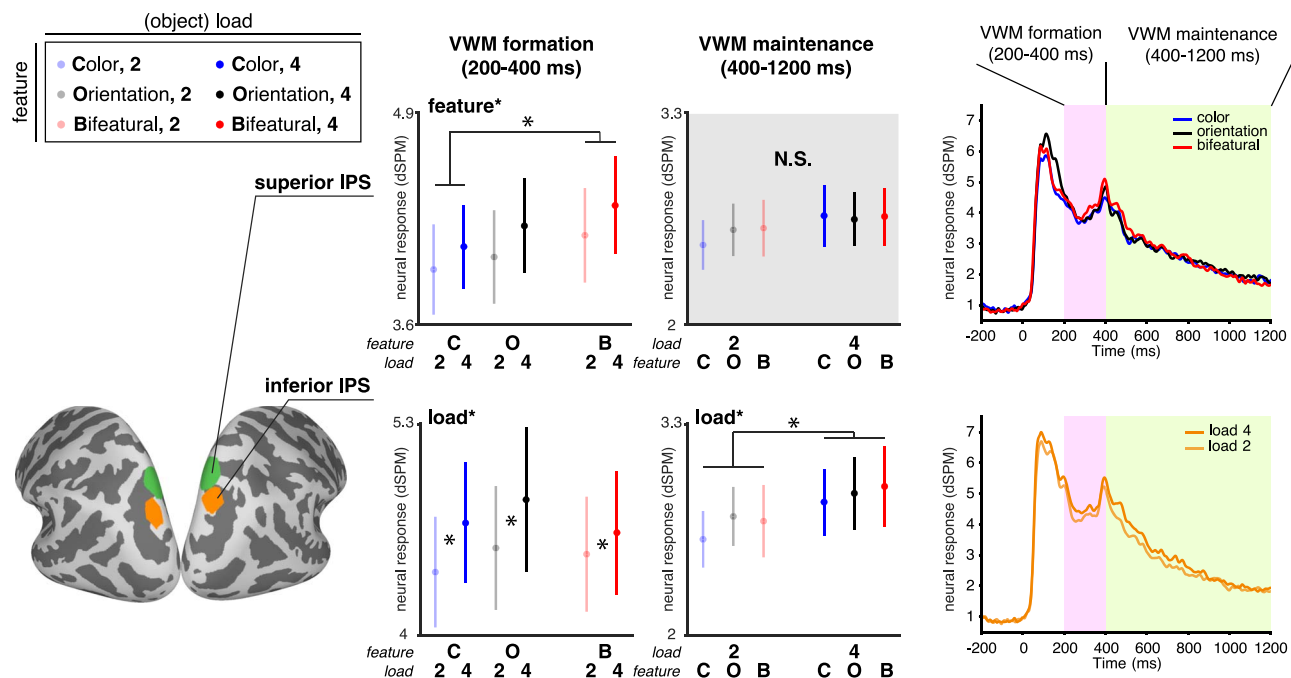


Figure 3 Leftmost and middle columns demonstrate responses during VWM formation (200 to 400 ms) and maintenance (400 to 1200 ms) in superior IPS and inferior IPS. The rightmost column demonstrates neural responses (dSPM) across time in the corresponding ROI grouped by feature or object load conditions. Error bars stand for standard error. *: $P \leq 0.05$. VWM: Visual working memory; ROI: Region of interest; IPS: Intraparietal sulcus; C: Color; O: Orientation; B: Bifeatural; 2: Object load = 2; 4: Object load = 4.

conditions. Therefore, we also conducted several complementary RSA analyses to gauge the robustness of our observations.

First, we conducted a similar analysis as in the previous section, but instead of 0, we coded the similarity between single-feature and bifeatural conditions as 0.5—between 0 and 1—to reflect the fact that bifeatural conditions contain both color and orientation, and to take into account a partial contribution of conjunctive coding across color and orientation, where the neural code for color and orientation is not simply a linear combination of the 2 single-feature representations (Sumner et al. 2008; Seymour et al. 2010). Still, we obtained qualitatively same results (Fig. 5a). For superior IPS, betas for object load and features were still reliably different from 0 for both VWM formation and maintenance: object load, VWM formation, $t(26) = 3.31$, FDR-adjusted $P_{FDR} = 0.003$, Cohen's $d = 0.64$; object load, VWM maintenance, $t(26) = 3.25$, $P_{FDR} = 0.003$, Cohen's $d = 0.63$; feature, VWM formation, $t(26) = 7.45$, $P_{FDR} < 0.001$, Cohen's $d = 1.43$; feature, and VWM maintenance, $t(26) = 4.81$, $P_{FDR} < 0.001$, Cohen's $d = 0.93$. For inferior IPS, betas for only feature were still different from 0: feature, VWM formation, $t(26) = 4.61$, $P_{FDR} < 0.001$, Cohen's $d = 0.89$; feature, VWM maintenance, $t(26) = 2.80$, and $P_{FDR} = 0.019$, Cohen's $d = 0.54$. Betas for object load also did not reach statistical significance: object load, VWM formation, $t(26) = 1.16$, $P_{FDR} = 0.33$, Cohen's $d = 0.22$; object load, and VWM maintenance, $t(26) = 0.99$, $P_{FDR} = 0.33$, Cohen's $d = 0.19$. The results held qualitatively when we coded the similarity between single-feature and bifeatural conditions in other values such as 0.2, 0.8, or 1 (see Supplementary Materials, Fig. S3).

Second, to better disentangle the total number of objects and the total number of features, we additionally included a similarity matrix for the total number of features to the analysis described in the previous paragraph. The results continued to hold qualitatively (Fig. 5b). For superior IPS, betas for object load and features were still different from 0 for both VWM formation and maintenance: object

load, VWM formation, $t(26) = 3.31$, $P_{FDR} = 0.005$, Cohen's $d = 0.64$; object load, VWM maintenance, $t(26) = 3.24$, $P_{FDR} = 0.005$, Cohen's $d = 0.62$; feature, VWM formation, $t(26) = 7.20$, $P_{FDR} < 0.001$, Cohen's $d = 1.39$; feature, and VWM maintenance, $t(26) = 4.41$, $P_{FDR} < 0.001$, Cohen's $d = 0.85$. Betas for the newly-added feature count similarity matrix were not statistically significant for either of the time windows, $P_{FDR} > 0.58$. For inferior IPS, still, betas for feature were different from 0, but not for object load: feature, VWM formation, $t(26) = 4.88$, $P_{FDR} < 0.001$, Cohen's $d = 0.94$; feature, VWM maintenance, $t(26) = 3.08$, $P_{FDR} = 0.015$, Cohen's $d = 0.59$; object load, VWM formation, $t(26) = 1.08$, $P_{FDR} = 0.47$, Cohen's $d = 0.21$; object load, and VWM maintenance, $t(26) = 0.87$, $P_{FDR} = 0.47$, Cohen's $d = 0.17$. Betas for the newly-added feature count similarity matrix were not statistically significant for either of the time windows, P_{FDR} 's > 0.47 .

Lastly, in line with recent studies (Chang et al. 2026), we also set up color load and orientation load similarity matrices separately, alongside representational similarity matrices on feature and object load. In line with Chang et al. (2026, experiment 2), collinearity induced instability in the estimation for other similarity matrices (see Supplementary Materials, Fig. S4). Indeed, the VIF for this RSA analysis is larger than the above 3 analyses: the first analysis (Fig. 4), the largest VIF across all variables $VIF_{\max} = 1.20$; the second analysis (Fig. 5a), $VIF_{\max} = 1.11$; the third analysis (Fig. 5b), $VIF_{\max} = 1.21$; and the current analysis, $VIF_{\max} = 2.41$. Taken together, our observations in section Multivariate analysis were qualitatively upheld across multiple configurations of RSA analyses.

Discussion

Using MEG, we examined univariate and multivariate neural responses for pointers and feature information in VWM, in 2 literature-driven posterior parietal patches: superior IPS and inferior

for each ROI, for each participant:

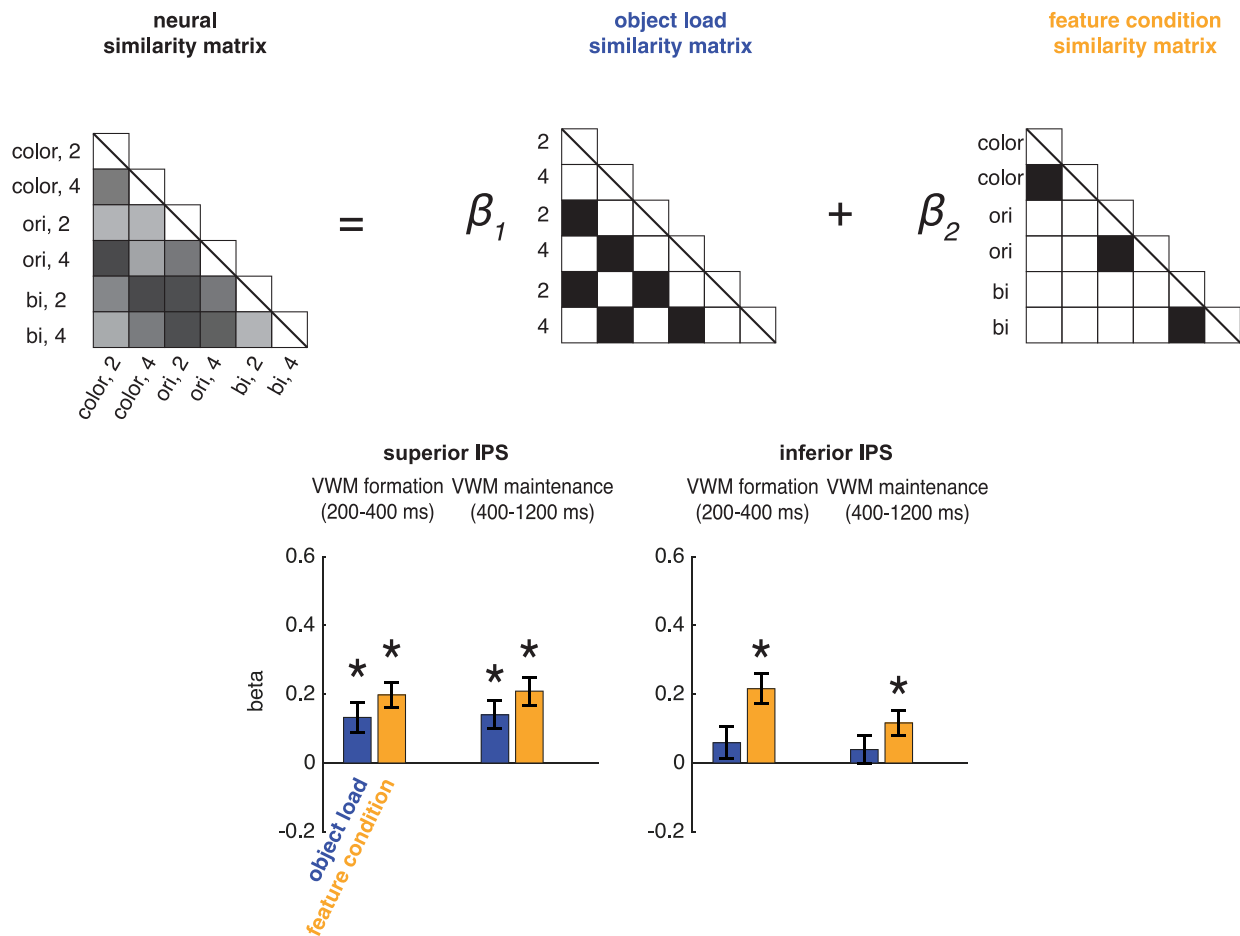


Figure 4 Multivariate representational similarity analysis (RSA) with object load and feature as factors. (Upper panel) Illustration of the similarity matrices and the multiple regression. Each matrix consisted of an array of values below the diagonal, z-scored prior to entering the multiple regression. (Lower panel) Beta values for each region-time window-factor combination, that are compared against 0 (2-tailed 1-sample t-test with FDR adjustment). *: $P \leq 0.05$.

Table 1 Summary of significant effects (marked with a tick and shaded in orange) observed in the current study (section Multivariate analysis).

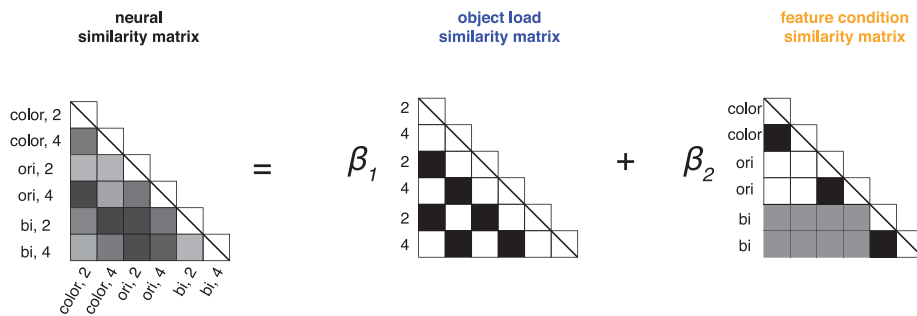
VWM formation (200 to 400 ms)				
	Pointer count		Feature information	
	Univariate signals	Multivariate signals	Univariate signals	Multivariate signals
Superior IPS		✓	✓	✓
Inferior IPS	✓			✓
VWM maintenance (400 to 1,200 ms)				
	Pointer count		Feature information	
	Univariate signals	Multivariate signals	Univariate signals	Multivariate signals
Superior IPS		✓		✓
Inferior IPS	✓			✓

IPS. Our results suggest an interesting neural response landscape across these 2 regions: the number of pointers is tracked in the inferior IPS by univariate signals, and in the superior IPS by multivariate signals. These observations hold across VWM formation

and maintenance, suggesting that these univariate and multivariate neural responses are both sustained across time. As for feature information, both IPS patches robustly reflect feature information during VWM formation and maintenance in multivariate signals.

(a)

for each ROI, for each participant:



(b)

for each ROI, for each participant:

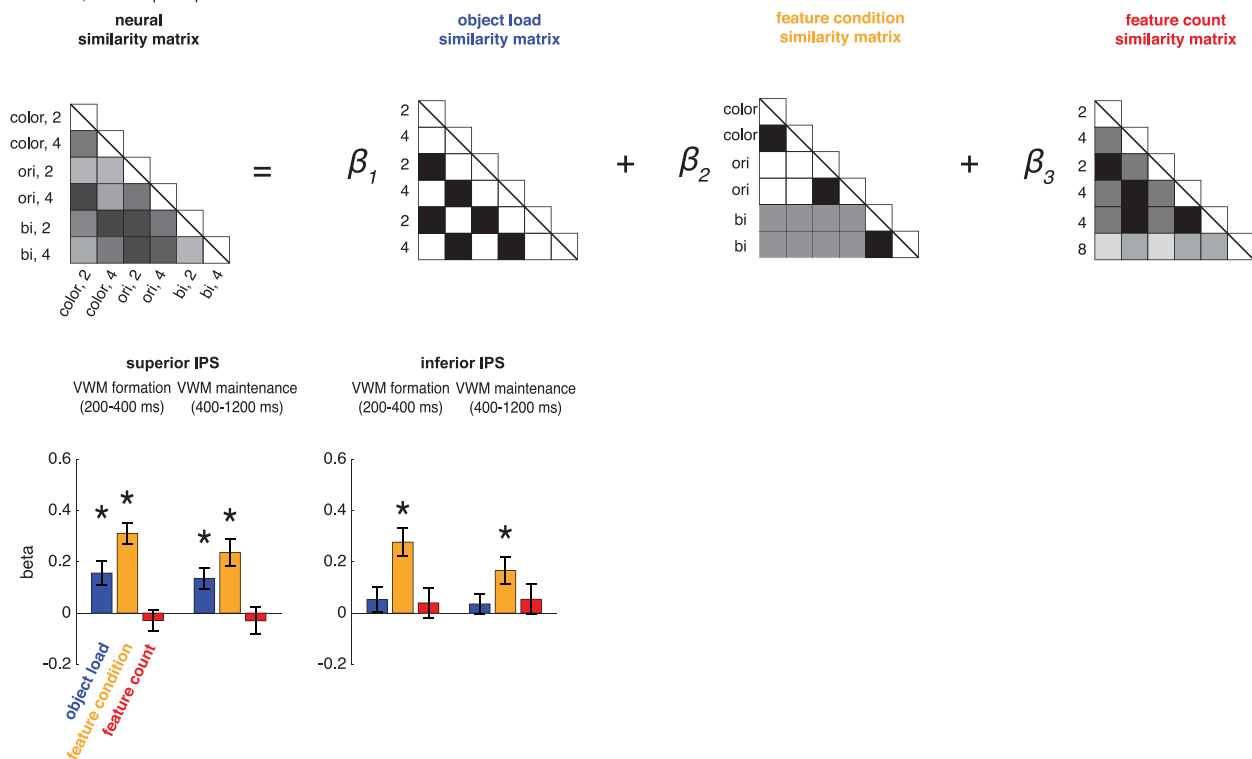


Figure 5 Multivariate representational similarity analysis (RSA) complementary analyses. a) Same analysis as Fig. 4, but coding the similarity between single-feature and bifeatural conditions as 0.5 (see section Complementary multivariate analyses). b) Analysis adding feature count as a factor, based on the analysis of (a). (Upper panels) Illustration of the similarity matrices and the multiple regression. Each matrix consisted of an array of values below the diagonal, z-scored prior to entering the multiple regression. (Lower panels) Beta values for each region-time window-factor combination, compared against 0 (2-tailed 1-sample *t*-test with FDR adjustment). *: $P \leq 0.05$.

Additionally, the number of features transiently manifests in superior IPS during VWM formation in univariate signals. Together, our results highlight that both univariate and multivariate neural responses in the posterior parietal cortex are relevant to VWM, and that the correspondence between univariate vs. multivariate signals and VWM pointers vs. features may differ across different subregions therein.

Relations with existing studies on visual working memory (VWM) pointers

As we outlined in the Introduction section, a diverse set of prior studies has reported univariate and multivariate neural signals for VWM pointers, and many of these studies were centered around inferior and superior IPS. The question thus arises of where and when the univariate and multivariate neural responses are hosted. Directly addressing this question with fMRI or EEG is challenging, as fMRI falls short in temporal resolution, and EEG falls short in spatial resolution. Leveraging MEG—a method with both acceptable spatial and temporal resolution—our current results reconcile previous reports. On the one hand, our results are in line with fMRI reports that univariate signals in inferior IPS but not superior IPS track the number of pointers (Xu and Chun 2006; Xu 2009). Here we show, with MEG's higher temporal resolution, that this effect holds for both VWM formation and maintenance. On the other hand, our results are also in line with EEG reports that multivariate signals track the number of pointers (Jones et al. 2024a; Jones et al. 2024b; Suplica et al. 2025). Taken together, these results enrich our understanding of the prior fMRI and EEG findings by showing that the relevance of univariate vs. multivariate neural signals depends on the subregion of IPS.

Relations with existing studies on feature information in visual working memory (VWM)

The existence of multivariate signals for feature information broadly in the IPS (which we observed in this study) is consistent with prior fMRI studies, where feature type was reliably decoded from multivariate signals in the IPS (Riggall and Postle 2012; Bettencourt and Xu 2016b; Lorenc et al. 2018; Teng and Postle 2024). Our observation of a transient univariate response in the superior IPS during VWM formation is also in line with prior fMRI studies (Xu and Chun 2006; Xu 2009), further refining the time window of this effect to VWM formation, as we did not observe a reliable effect of feature information during VWM maintenance. This observation is also broadly consistent with studies on univariate signals in EEG and MEG studies on VWM: in contrast to robust modulations of univariate effects (eg CDA [contralateral delay activity], NSW [negative slow wave], or RPA) by object load, many studies fail to observe significant effects of feature information on univariate signals (Woodman and Vogel 2008; Luria and Vogel 2011; Shen et al. 2013; Guo et al. 2025; Yu and Lau 2025c).

Our current results are partially consistent with a previous fMRI study that also compared univariate vs. multivariate responses for VWM pointers and their features (Naughtin et al. 2016). Following Xu (2009), Naughtin et al. (2016) leveraged 3 experimental conditions: a 1-item condition, a 4-item condition with identical items, and a 4-item condition with different items. The 1-item condition and the 4-item identical condition thus shared the same number of total feature counts but differed in the number of pointers, while the 4-item

identical condition and the 4-item different condition shared the same number of pointers but differed in the total feature count. As in the current study, Naughtin et al. (2016) observed univariate signals in the inferior IPS tracking the number of pointers, and univariate signals in the superior IPS tracking the number of features. For multivariate signals, using a decoding approach, Naughtin et al. (2016) decoded above-chance level across 4-item identical vs. 4-item different conditions in both superior and inferior IPS, again consistent with the current results. The only point of difference from the current study is that Naughtin et al. (2016) additionally reported univariate signals in the superior IPS and multivariate signals in the inferior IPS differentiating 1-item and 4-item identical conditions. Two factors may explain this discrepancy. One is that the superior IPS ROI in the Naughtin et al. (2016) study extended beyond Xu and Chun's (2006) ROI, incorporating a larger region extending into the superior parietal lobe. The other related factor is that a larger ROI was used for multivariate decoding compared to the univariate analysis in their study. Therefore, the additional effects observed by Naughtin et al. (2016) may reflect contributions from neighboring regions. This was corroborated by additional analyses on our current dataset using a larger ROI: indeed, the multivariate signals tracking the number of objects in the inferior IPS came out when employing a larger ROI (see Supplementary Materials).

One further general limitation with fMRI VWM studies worth noting is that, to temporally disentangle VWM formation and maintenance, the delay period in fMRI studies needs to be very long (12.8 s for Naughtin et al. 2016) due to slow blood-oxygen-level-dependent (BOLD) response functions. This is much longer than canonical behavioral or EEG/MEG studies on VWM (delay period usually less than 2 to 3 s), and therefore performing a VWM task under these conditions may well involve different or additional cognitive representations or processes (Fukuda et al. 2015).

Univariate and multivariate codes: what are they good for?

In the current study, we discovered that in the posterior parietal cortex, both univariate signals and multivariate signals track the number of VWM pointers. Feature information also manifests as both univariate and multivariate signals. Indeed, observing a relation between a certain neural response and a variable does not necessarily entail that this neural response is actively read out by downstream regions or operations (Ritchie et al. 2019; Peelen and Downing 2023), but this type of observation offers crucial evidence that the neural responses in this brain region can be read out in principle.

If we take our observations to suggest that both univariate and multivariate *neural codes* are implemented for VWM representations, a curious question is naturally invited: why does the brain need complementary univariate and multivariate codes? To speculate, these two coding schemes may have their pros and cons respectively. For univariate coding, an increase in the number of pointers accompanies an increase in global neural activation level, implicating an increase in energy consumption. In contrast, multivariate coding can be more energy-efficient, as the multivariate code can be distinctive for different numbers of pointers while keeping constant the overall activation level (cf. Wang 2021). What is multivariate coding bad at, then? One possibility is that multivariate coding has a lower signal-to-noise ratio compared to univariate coding. This possibility arises from a key observation in systems neuroscience, that compared to the number of potentially informative neurons in each brain module, the number of

connections between two brain modules is magnitudes smaller (Lin et al. 2023). This suggests that reading out multivariate signals from a certain region may be very lossy due to a limited sampling among the potentially-informative neurons. In contrast, univariate signals—which reflect the aggregate activity of a population—would be much more robust to such sampling limitations. Intriguingly, recent work reveals monosynaptic connections between the posterior parietal cortex and non-adjacent regions (Xu et al. 2026); in these cases univariate representation appears to be a better engineering design compared to multivariate representation.

While not being able to adjudicate based on our current study, there are many interesting possibilities for why complementary univariate and multivariate signals underlie VWM representations. For example, for the same memorandum, different VWM representations in the brain are differentially susceptible to distraction (Bettencourt and Xu 2016b). This might map onto differential susceptibilities to distraction for univariate and multivariate signals. For example, multivariate signals may be more robust against distraction, as the targets and distractors can be represented in different subspaces in a high-dimensional space (Xu 2024). Another possibility is that univariate and multivariate representations may differ in their flexibilities, for example, in adjusting priorities across memorized items, with multivariate representations potentially being more flexible (Wan et al. 2024). These interesting theoretical and functional possibilities should be directly tested in future work.

Furthermore, although univariate and multivariate signals and pointer and feature signals are sometimes simultaneously identified within the same subregion of the IPS, a remaining question is whether these representations are realized by overlapping or distinct cohorts of neurons. This could be resolved by intracranial recordings, which provide resolution at the single neuron scale. Further theoretical interpretation would depend on whether univariate and multivariate signals, and whether pointer and feature signals, share overlapping or distinct connectivity profiles with other brain regions. It is certainly plausible that different neural formats (univariate, multivariate) and brain regions track attention-related processes and VWM pointers separately, which would be interesting to disentangle in future studies (for more discussion, see section Limitations and future directions).

In all, the complementarity of univariate and multivariate coding schemes may offer neural redundancy that overcomes the limitations of each coding scheme. A complementarity of univariate and multivariate codes is also likely a general coding principle supporting cognition, beyond the scope of VWM (Yang et al. 2022; Yu et al. 2025). Note that there is yet another possible format of representation (“activity-silent mechanisms”) that does not necessarily incur any neural firing, realized for example via synaptic connectivities (Wolff et al. 2015; Rose et al. 2016) or intracellular coding (Gallistel and King 2009; Akhlagpour 2022; Lau 2025).

The nature of visual working memory (VWM) representations

A large body of research has debated the nature of VWM representations and the capacity limit of VWM (for a recent review see Ngiam 2024). While some theories posit that VWM capacity is best characterized by the number of objects (Awh et al. 2007; Zhang and Luck 2008; Adam et al. 2017), and some theories posit that this capacity is best modeled with both the number of objects and features (Wheeler and Treisman 2002; Fougine et al. 2010), virtually no theory would

argue that VWM representation is *only* composed of free-floating features. Most, if not all, influential theories on VWM acknowledge the necessity of both feature representations and binding resources that bind some features together to form representations for objects (Ngiam 2024). In this light, we do not consider our current MEG study to be testing different neuro-cognitive models of VWM, but instead to inform us about how different aspects of VWM representations are realized in the brain.

Meanwhile, a growing body of literature focuses on the distributed nature of VWM representation across the brain, underscoring the relevance of many other brain regions beyond the IPS (Lee and Baker 2016; Naughtin et al. 2016). While a comprehensive region-by-region analysis across the entire brain (Adam et al. 2025) would be extremely interesting and would be a next step for our research, this is beyond the scope of the present article primarily driven by the line of fMRI literature on subregions within the IPS. To demonstrate an effort along this line, we additionally analyzed univariate and multivariate responses in the early visual cortex in the Supplementary Materials, following a long-standing interest in the early visual cortex’s role in VWM (Ester et al. 2009; Xu 2017).

Limitations and future directions

A remaining interpretive question concerns what exactly the object load-sensitive signals reflect. In our design, the number of pointers covaries with the number of attended locations and with the spatial extent of the area that has to be attended, so we cannot distinguish whether these signals index location-independent pointers or location-based object individuation (Xu and Chun 2009; Naughtin et al. 2018), nor can we distinguish between working memory and spatial attention. What these accounts all acknowledge is a representation or operation that is dissociable from the representation of non-spatial features, and in the current study, we uncovered the spatiotemporal dynamics and candidate neural formats (univariate, multivariate signals) of this critical representation or operation. However, an important direction for future work is to consider how to disambiguate exactly which of these representations and processes drive the MEG responses reported here.

Recent EEG studies have developed paradigms aimed at disentangling spatial attention effects from effects of the number of pointers, for example by presenting objects sequentially at the same versus different locations (Jones et al. 2024a), or at the same locations while varying whether they can be perceptually grouped (Thyer et al. 2022). A single-location sequential presentation was also included in Xu and Chun (2006, experiment 4), which yielded a null effect of object number on the univariate response of the inferior IPS. While this result might be taken as evidence that inferior IPS activity reflects pointer maintenance rather than spatial attention, we note that there are also some caveats to the interpretation of sequential presentation designs. First, sequential presentation tends to disrupt sustained neural activities unless the task explicitly encourages otherwise (Feldmann-Wüstefeld et al. 2018; Zhang et al. 2022), which may reflect a shift in representational format from VWM toward longer-term storage. Second, presenting 2 objects sequentially at the same location can be construed as a single object changing its features over time rather than as 2 distinct objects, or as 2 genuinely different objects (Park et al. 2020). On balance, we regard the positive evidence for a location-independent object-count signal (eg Jones et al. 2024a) as more compelling than the null findings. The 4-identical- versus 4-different-object manipulation of Naughtin et al. (2016)—following a

similar logic—is also ambiguous, as participants may differ in whether they strategically encode repeated identical items as 1 object or as 4 (Gao et al. 2011), and the extent to which they actively encode the locations when identical items appear at multiple locations. However, because positive neural differences were observed across these 2 conditions, at least some of the participants must have encoded repeated identical objects with multiple pointers and/or locations.

Building on the evidence reported here, future MEG studies should incorporate these relevant manipulations systematically—for example sequential presentation and grouping—to disentangle the number of pointers from the number of locations and the breadth of spatial attention. Such work would clarify whether the complementary univariate and multivariate codes we observe track pointers per se, or the spatial-attentional operations that may be required to establish and sustain them (Xu and Chun 2009).

Conclusion

In sum, our current MEG study revealed complementary neural response profiles for VWM objects vs. features in the posterior parietal cortex: in inferior IPS, univariate signals track the number of objects, while in superior IPS, the number of objects is tracked by multivariate signals. This complementary neural response landscape reconciles prior reports of either univariate or multivariate neural responses for VWM pointers. Feature information is reflected in multivariate signals across superior and inferior IPS, and the number of features is additionally reflected in univariate signals in superior IPS during VWM formation. Taken together, our current study refines our understanding on how the brain supports different aspects of VWM with complementary formats and neural responses.

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Author contributions

Xinchi Yu (Conceptualization [equal], Methodology [equal], Software, Formal analysis, Investigation, Data curation, Writing—original draft, Writing—review & editing [equal], Visualization) and Ellen Lau (Conceptualization [equal], Methodology [equal], Resources, Writing—review & editing [equal], Supervision, Funding acquisition)

Supplementary material

Supplementary material is available at *Cerebral Cortex* online.

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Conflicts of interest

The authors declare no conflict of interest.

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