

JYX



**This is a self-archived version of an original article. This version may differ from the original in pagination and typographic details.**

**Author(s):** Liang, Tengfei; Chen, Xiaoyu; Ye, Chaoxiong; Zhang, Jiafeng; Liu, Qiang

**Title:** Electrophysiological evidence supports the role of sustained visuospatial attention in maintaining visual WM contents

**Year:** 2019

**Version:** Accepted version (Final draft)

**Copyright:** © 2019 Elsevier B.V.

**Rights:** CC BY-NC-ND 4.0

**Rights url:** <https://creativecommons.org/licenses/by-nc-nd/4.0/>

**Please cite the original version:**

Liang, T., Chen, X., Ye, C., Zhang, J., & Liu, Q. (2019). Electrophysiological evidence supports the role of sustained visuospatial attention in maintaining visual WM contents. *International Journal of Psychophysiology*, 146, 54-62. <https://doi.org/10.1016/j.ijpsycho.2019.09.011>

## Journal Pre-proof

Electrophysiological evidence supports the role of sustained visuospatial attention in maintaining visual WM contents

Tengfei Liang, Xiaoyu Chen, Chaoxiong Ye, Jiafeng Zhang, Qiang Liu



PII: S0167-8760(19)30504-5

DOI: <https://doi.org/10.1016/j.ijpsycho.2019.09.011>

Reference: INTPSY 11646

To appear in: *International Journal of Psychophysiology*

Received date: 15 April 2019

Revised date: 13 August 2019

Accepted date: 26 September 2019

Please cite this article as: T. Liang, X. Chen, C. Ye, et al., Electrophysiological evidence supports the role of sustained visuospatial attention in maintaining visual WM contents, *International Journal of Psychophysiology*(2019), <https://doi.org/10.1016/j.ijpsycho.2019.09.011>

This is a PDF file of an article that has undergone enhancements after acceptance, such as the addition of a cover page and metadata, and formatting for readability, but it is not yet the definitive version of record. This version will undergo additional copyediting, typesetting and review before it is published in its final form, but we are providing this version to give early visibility of the article. Please note that, during the production process, errors may be discovered which could affect the content, and all legal disclaimers that apply to the journal pertain.

© 2019 Published by Elsevier.

**Electrophysiological evidence supports the role of sustained visuospatial attention in maintaining visual WM contents**

Tengfei Liang<sup>a,b</sup>, Xiaoyu Chen<sup>b</sup>, Chaoxiong Ye<sup>a,c</sup>, Jiafeng Zhang<sup>b</sup>, Qiang Liu<sup>a,b</sup>

<sup>a</sup>Institute of Brain and Psychological Sciences, Sichuan Normal University, *Chengdu, 610000, China.*

<sup>b</sup>Research Center of Brain and Cognitive Neuroscience, Liaoning Normal University, *Dalian 116029, China.*

<sup>c</sup>Department of Psychology, University of Jyväskylä, *Jyväskylä, 40014, Finland*

Corresponding author:  
Qiang Liu

E-mail: lq780614@163.com

Institute of Brain and Psychological Science, Sichuan Normal University, Chengdu,  
610000, China.

**Abstract**

Recent empirical and theoretical work suggests that there is a close relationship between visual working memory (WM) and visuospatial attention. Here, we investigated whether visuospatial attention was involved in maintaining object representations in visual WM. To this end, the alpha lateralization and contralateral delay activity (CDA) were analyzed as neural markers for visuospatial attention and visual WM storage, respectively. In the single-task condition, participants performed a grating change-detection task. To probe the role of visuospatial attention in maintaining WM contents, two color squares were presented above and below the fixation point during the retention interval, which remained visible until the detection display was present. In the dual-task condition, participants were required to maintain lateralized gratings while staring at the center-presented color squares, to detect possible subsequent color change. With this task, sustained visuospatial attention that guided to individual memory representations was disrupted. The behavioral data showed that, the insertion of secondary task significantly deteriorated WM performance. For electrophysiological data, we divided the retention interval into two stages, the early stage and late stage, bounded by the onset of the secondary task. We found that CDA amplitude was lower under the dual-task condition than the single-task condition during the late stage, but not the early stage, and the extent to which CDA reduced tracked the impaired memory performance at the individual level. Also, alpha lateralization only could be observed in the single-task condition of the late stage, and completely disappeared in the dual-task condition, indicating the disruption of visuospatial attention directed to memory representations. Individuals who experienced greater visuospatial attention disruption, as indicated by the alpha lateralization, had lower maintenance-associated neural activity (CDA), and suffered greater impairment of memory performance. These findings confirm that sustained visuospatial attention continues improving visual WM processing after the initial encoding

phase, and most likely participates in this process by supporting the maintenance of representations in an active state.

*Keywords:* visual working memory, visuospatial attention, alpha lateralization, contralateral delay activity

Journal Pre-proof

## 1. Introduction

The visual working memory (WM) is a system that temporarily holds invisible visual information “online” to support them to be easily accessed and manipulated. In recent years, an influential “activity-silent” model posits that the visual WM contents can be maintained in different representational states, supported by distinct neural mechanisms (Itskov et al., 2011; Mongillo et al., 2008; Stokes, 2015). In this view, memory contents in the active state are maintained by persistent neural activity, while information not related to the current goal can be supported via rapid synaptic plasticity (Mongillo et al., 2008; Rose et al., 2016; Stokes, 2015; Stokes et al., 2013; Wolff et al., 2015, 2017; but see also Christophel et al., 2018), thus allowing the neural network to enter a short silent stage. In line with this view, researchers found that the memory item related to the current goal elicits an active neural trace in the sensory area (LaRocque et al., 2017; Nee and Jonides, 2013; Zokaei et al., 2014), while neural activity of the unrelated item was reduced to baseline level. However, if the unrelated item become relevant again, persistent, stimulus-specific delay activity can be restored (LaRocque et al., 2013). Nevertheless, memory items in active state, which relies on continuous neural activity, can be maintained with high fidelity (Emrich et al., 2013; Ester et al., 2013).

According to the sensory recruitment hypothesis (Harrison and Tong, 2009; Serences et al., 2009), the active state of WM representations are suggested to be stored in the posterior sensory areas. During the delay interval, in the absence of visual stimuli input, the sustained stimulus-specific activity in the occipital cortex was used as the main evidence to support this hypothesis (Albers et al., 2013; Gayet et al., 2017; Harrison and Tong, 2009; Sneve et al., 2012). Not only visual information, but the short-term storage of other modalities were also found in a way of sensory recruitment

(Schmidt et al., 2014; Schmidt and Blankenburg, 2018). Therefore, the same sensory regions that encode the sensory signals also mediate the temporary retention of these information (Pasternak and Greenlee, 2005). However, not all representations in visual WM is maintained in the way of sensory recruitment. Only item within the current focus of attention can be decoded from patterns of persistent neural activity in the sensory region (Harrison and Tong, 2009; Lewis-Peacock et al., 2012; Sreenivasan et al., 2014), neural activity of the representations outside the focus of visual attention decreases to baseline level, suggesting that sensory recruitment hypothesis is closely related to the participation of visuospatial attention.

In this study, we explored another issue related to the sensory recruitment hypothesis. Specifically, we further examined whether the maintenance of visual information in WM engaging sustained visuospatial attention. In perceptual processing, attention to the perceptual scenes has been metaphorized as a spotlight or a zoom lens mechanism (Posner and Petersen, 1990). Visual stimuli illuminated by the spotlight are considered to be better perceived (Brefczynski and DeYoe, 1999; Posner, 1980; Posner and Petersen, 1990), and accompanied by enhanced stimuli-specific neural activity in the occipital cortex (Bays, 2014; Wang et al., 2015). In the field of visual WM research, it has been proved that visuospatial attention plays an important role in the encoding and consolidation process. For example, attention to a spatial position facilitates consolidation of the item in that position into visual WM (Belopolsky et al., 2008; Infanti et al., 2015; Schmidt et al., 2002). Besides, the distribution of visuospatial attention between objects during encoding affects subsequent WM performance (Emrich et al., 2017). If the active state memory representations are equivalent to “reasonable copies” of scenes constructed during sensory processing, as the sensory recruitment hypothesis claimed, then sustained visuospatial attention may also support maintaining these items in high-fidelity representations with the help of item-specific

delay activity. However, some researchers tend to believe that maintaining information in visual WM is independent of the visuospatial attention. As supporting evidence, they found that subsequent visual WM performance remained intact when visuospatial attention was disrupted during the retention interval.

In a study of Maxcey-richard and Hollingworth (2013), for example, participants were sequentially presented with multiple sample items, one of which was transferred to the active state with the help of retro-cue. They found that the cued item was well maintained, even though visuospatial attention was disrupted by the subsequent sample arrays. This finding, they argued, could serve as evidence that the strategic retention of task-relevant WM content being dissociable from the current locus of visuospatial attention. Soon afterwards, Maxcey-richard and Hollingworth obtained further evidence in another study, wherein a retro-cue was presented during the delay interval of a change-detection task (Hollingworth and Maxcey-Richard, 2013). After the offset of the retro-cue, a visual search task expropriating sustained visuospatial attention also needs to be performed. They found that the retro-cue benefit was immune to the inserted secondary task. Similar results were also obtained by Rerko et al. (2014). In their experiment 1, the brightness change-detection task was used to disrupt the normal use of visuospatial attention in the maintenance of object representations, in which participants were required to monitor the fixation cross for a potentially small change in brightness. They found that the retro-cue benefits remained intact under the dual-task condition. Furthermore, in other visual WM studies using traditional change detection task, visuospatial attention task inserted during the retention interval also had no effect on subsequent memory performance (Kiyonaga et al., 2017; Souza and Oberauer, 2017; Woodman et al., 2001; but see Williams et al., 2013). However, it is worth noting that the experimental design of these studies might allow the release of visuospatial attention before the memory probe was presented. For example, in the studies of Hollingworth



and Maxcey Richard, at least one second was allowed for subjects to refocus their visuospatial attention on related memory items before the detection stage. In experiment 1 of Rerko et al. (2014), the time interval between the end of the secondary task and the onset of the memory probe was also at least 0.7s. Consider that guiding visuospatial attention to a working memory representation can occur in just 0.3s (Gressmann and Janczyk, 2016; Pertzov et al., 2012; Tanoue and Berryhill, 2012), the non-occupied time intervals of these studies might allow for the re-entry of visuospatial attention, and made it possible to refresh memory representations before the memory probe was presented, taking into account the notion that refreshing operates through a process of retrieving memory items into the focus of attention (Barrouillet and Portrat, 2011; Vergauwe and Cowan, 2015), and thus leading to observed zero results.

Here, we continued to examine the role of visuospatial attention in maintaining visual information in WM using the dual-task paradigm. To prevent the re-entry of visuospatial attention during the late retention stage, we canceled the time interval between the secondary task and the memory probe. To do this, we used the continuously present change detection task invented by Tsubomi et al. (2013) as the visuospatial attention task. In their experiment, the color arrays did not disappear during the delay interval until a color change was occur. Therefore, successful detection of color changes does not require observers to remember the persistently visible stimuli in any traditional means, but simply maintain them within view with no additional cognitive processes (Tsubomi et al., 2013). Besides, since no additional response was required during the retention interval, the involvement of the central attention could also be reduced (Johnston et al., 1995). Under the dual-task condition, participants needed to maintain the lateralized memory items while continuously staring at the centrally-presented visible stimuli presented during the delay interval (see the procedure section for detailed task description), which tapping sustained visuospatial attention. In order to

eliminate mutual interference between WM contents and perceptual input in the representation space (Clapp et al., 2010), we used gratings in the main visual WM task, which was different from the color squares used in secondary task. Woodman and Vogel (2005) found that it takes about 100-msec to consolidate a grating into visual WM. In our experiment, there was 400-msec between the onset of the memory arrays and the color squares. According to their evidence, the consolidation of two gratings in the current experiment could be completed before the onset of the secondary task. Therefore, this setting ensured that the disruption of visuospatial attention only affected the retention stage of WM task.

We hoped to observe the neural dynamics of the association between sustained visuospatial attention and the online maintenance of visual WM in real time. To this end, high time resolution electrophysiological data was collected synchronously. Considering that the persistently visible color squares were presented vertically and memory arrays laterally, the lateralized activities observed during the retention period could only reflect the WM-related processing. We focus on two lateralized EEG indicators, alpha lateralization and contralateral delay activity (CDA). The former is able to track the locus of covert visuospatial attention (Ikkai et al., 2016; Klatt et al., 2018; Poch et al., 2017, 2018; Sauseng et al., 2005; Thut et al., 2006; Worden et al., 2000), while the latter varies with the active maintenance processing in visual WM, and is sensitive to individual differences in WM capacity (Feldmann-Wüstefeld et al., 2018; Luria et al., 2016; Vogel and Machizawa, 2004). We predict that the inserted secondary task during the retention interval would disrupt the normal use of visuospatial attention in maintaining object representations and result in impaired memory performance. To establish whether the participation of visuospatial attention was associated with visual WM processing, correlations between the modulation of alpha lateralization and CDA following the onset of the secondary task and the modulation of memory performance

were computed. Weaker alpha lateralization in dual-task condition compared to single-task condition, indicating more serious disruption of visuospatial attention, was expected to be associated with stronger CDA modulation and greater performance deterioration.

## 2. Materials and methods

### 2.1. Participants

Twenty-six healthy young adults (13 male, age 18-26, two left-handed) took part in this experiment. All the participants reported no neurological or psychiatric history and had normal or corrected vision. Each participant voluntarily enrolled and signed an informed consent form prior to the experiment. We based our sample size on the study by Xie and Zhang (2017) that compared CDA amplitudes produced under two different conditions with an equal memory load. The effect sizes from their study (*Cohen's*  $d = 0.87$ ) indicated that, to detect the differences in CDA amplitudes between two conditions with equal memory load, a minimum of thirteen participants would be necessary to achieve 80% power. Four participants were excluded due to poor performance, excessive eye movements, or other electroencephalogram (EEG) artifacts. The experiment was carried out in accordance with the Declaration of Helsinki and was approved by the institutional ethics committee of the Liaoning Normal University.

### 2.2. Stimuli

The stimuli were presented with E-Prime software on a 17-inch LCD monitor (60-Hz refresh rate, 1920×1080 pixel). Participants were seated in a sound-attenuated recording chamber at a viewing distance of 90 cm. All experimental stimuli were presented on a gray background. The secondary task consisted of two-color squares ( $1.32^\circ \times 1.32^\circ$ ), which were randomly placed at the top and bottom of the fixation point ( $4.95^\circ$  from the central fixation).

The color of each stimulus was randomly selected from a set of eight colors (blue, magenta, black, lime, red, cyan, white, and yellow) with the given color appeared only once in the arrays. In each trial, four circular gratings (size,  $1.2^\circ$ , contrast, 3.7; spatial frequency, 4 cycles/deg) were presented on four fixed locations, which were arranged on an imaginary circle with a radius of about  $4.95^\circ$ . The orientation of each grating was randomly selected from six possible angles:  $10^\circ$ ,  $40^\circ$ ,  $70^\circ$ ,  $100^\circ$ ,  $130^\circ$ , and  $160^\circ$ . The edges of the apertures were smoothed, which avoided sharp changes in brightness between grating and the background.

<PLEASE INSERT FIGURE 1 HERE>

### 2.3. Procedure

As in Figure 1, each trial began with a 200 msec cue presented over the fixation point, pointing either to the left or the right. After a random interval of 500-800 msec, four gratings with different orientations (i.e. the memory arrays) were presented for 200 msec, distributed in pairs on both sides of fixation point. After a 200 msec blank interval, the color squares (i.e. the attended stimuli) were presented above and below the fixation point and continued to be visible (with a delay of 700 msec) until the detection display was presented. The current experiment has two different sessions, whose order was counterbalanced across participants. For the dual-task session, when the detection display was presented, there were two possible cases, with a probability of 50% each. In the case of the memory detection, participants were presented with a probe grating at one of the locations previously occupied by memoranda. In the trials of “unchanged”, the probe had the same orientation as the memory grating at that position. Whereas in the trials of “changed”, the probe had an orientation difference  $90^\circ$ . In this task, participants needed to judge whether the orientation

of the probe grating was the same as the memory grating. In the case of the attention detection, participants were presented with a color probe at one of the attended locations. The probe was consisted of two rectangles with half the width of the attended color squares. In the trials of “unchanged” , one rectangle remained the same color as the attended color square at that position, and the other one was filled with a new color. In the trials of “changed” , both rectangles were filled with new colors. In this task, participants needed to detect whether one of the two rectangles that made up the probe retained the color of the attended color square in the same position. For the single-task session, only the memory probe was presented, and participants were told to ignore the color squares. The “changed” trials and “unchanged” trials corresponded to different keys respectively, and two kinds of trials were presented randomly with equal probability. Participants gave an unspeeded response. The next trial began 1000 msec after participants responded.

Each session was provided with an appropriate instruction to ensure that the participants knew in advance whether the attended color square would be detected (i.e. the secondary task). Participants were given at least sixteen practice trials before each session with direct performance feedback at the end of each trial. Each session was split into six mini-blocks of 48 trials each, with a break of at least 20s between mini-blocks. Participants completed a total of 576 experiment trials.

#### 2.4. EEG recording and analysis

The EEG was recorded by using the ANT-NEURO system (Enschede, The Netherlands) with 64 Ag/AgCl electrodes arranged in a 10/20 system layout (including left and right mastoids, AFz serving as ground, and CPz serving as the on-line reference). Horizontal eye movements were recorded by electrodes placed on the outer canthi of the right and left eyes,

and vertical eye movements were recorded from Fpz electrode to detect blinks. The impedances of the electrodes were maintained below 10 k $\Omega$ . Data were digitized at 500 Hz.

EEGLAB Toolbox (Delorme and Makeig, 2004) and custom MATLAB scripts were used for off-line processing (MATLAB 2014a, The MathWorks, Natick, MA). Data were firstly low-pass filtered at 40 Hz and re-referenced offline to an average of the mastoids, and then epoched from 500 msec before the memory array onset to 1,100 msec after the memory array onset. Trials with eye movements (exceeding  $\pm 50$   $\mu$ V in the HEOG channels), eye blinks (exceeding  $\pm 80$   $\mu$ V at Fpz), and excessive noise or drift (exceeding  $\pm 100$   $\mu$ V for the analyzed electrodes) were rejected. Both correct and incorrect EEG trials were included in the statistical analysis, as the removal of incorrect trials did not change the pattern of results, but would have reduced the signal-to-noise ratio of EEG data.

## 2.5. Analysis of CDA

For the ERP analysis, the averaged EEG epochs for the 1,100-ms interval following the memory array onset were computed relative to a 200-msec pre-stimulus baseline. CDAs were calculated by subtracting the average of the ipsilateral electrodes from the average of the contralateral electrodes. To analyze CDAs, we separately averaged the ERPs of six electrodes at parieto-occipital scalp regions (PO7/8, PO5/6, P3/4, P5/6, P7/8, CP5/6). These electrodes well cover the areas of energy concentration in the scalp distribution of CDA and the alpha lateralization, which take advantage of the fact that component and time-frequency effects typically extend over multiple consecutive sample points and multiple adjacent sensor sites (see Figure 3C-D).

## 2.6. Analysis of alpha lateralization

For the time-frequency analysis, the single-trial EEG signal (processed data) was convolved with complex Morlet's wavelets (Kronland-Martinet et al., 1987). Using the `cwt.m` function in the wavelet toolbox in MATLAB, instantaneous power was extracted on the entire epoch. Percent change in alpha power was calculated relative to a baseline period before the onset of the memory array (-400 to -100 msec). Alpha lateralization was calculated by subtracting the percent change waveform of alpha band (8-12 Hz) for ipsilateral electrodes from the contralateral electrodes. We calculated alpha lateralization for the same parieto-occipital electrodes as CDA.

## 2.7. Statistical analysis

In all of our F analyses in which the assumption of sphericity was violated, the Greenhouse-Geisser correction for nonsphericity was applied. We conducted Student's t-test for paired samples. Cohen's *d* (Cohen, 1977) and its confidence interval (Cumming and Fidler, 2009) were reported in order to provide more detailed information to support the conclusion. Cohen's *d* was calculated by dividing the mean difference by the pooled standard deviation method. All statistical analysis was done in JASP software (Marsman and Wagenmakers, 2017).

To determine statistical significance and investigate the dynamic impact of secondary task on visual WM processing, the time series for CDA and alpha lateralization for each condition were tested against chance and also against each other at a group level using non-parametric group-level permutation test (Maris and Oostenveld, 2007). with cluster correction for multiple comparisons (the threshold of cluster-defining and corrected

significance level were set to  $p < 0.05$ ). All tests were carried out in a more rigorous two-sided manner.

### 3. Results

#### 3.1. Behavioral results

As shown in Figure 2A, the percentage correct for attention task was  $81.20 \pm 1.86\%$ , which was significantly higher than the chance level,  $t(21) = 16.79$ ,  $p < 0.001$ , cohen's  $d = 3.58$ , 95% CI = [2.42, 4.73], demonstrating that participants were actively engaged with this task. The percentage correct of WM task in both conditions were converted to a capacity score  $K$  (Cowan, 2001), calculated as  $K = S \times (P - 50) / 50$ , where  $S$  is the set-size, and  $P$  is percentage correct (Tsubomi et al., 2013). The paired sample t-test showed that memory performance of  $K$  values sharply decreased for dual- ( $0.91 \pm 0.12$ ) relative to single-task condition ( $1.40 \pm 0.07$ ),  $t(21) = -4.72$ ,  $p < 0.001$ , cohen's  $d = 1.01$ , 95% CI = [0.48, 1.51]. This result means that the deprivation of visuospatial attention led to impaired memory performance.

<PLEASE INSERT FIGURE 2 HERE>

#### 3.2. Electrophysiological results

##### 3.2.1. CDA

We examined typical neural correlation of the real-time effects of attention task on visual WM processing, using CDA amplitude as the neural marker of online storage. Considering that the secondary task was presented in the 400 msec after the onset of the memory arrays, we divided the retention stage of WM task into two intervals, namely, the early stage (300-500 msec) before and the late stage (600-1100 msec) after the secondary task was presented. As Figure 3A shows, both conditions produced



comparable CDA amplitudes until the late stage after the secondary task was presented. We confirmed this impression with a repeated measures ANOVA including the factors condition (single- vs. dual-task) and retention stage (early vs. late). This analysis revealed a significant main effect of condition,  $F(1, 21) = 5.33, p < 0.031, \eta^2 = 0.20$ , retention stage,  $F(1, 21) = 32.73, p < 0.001, \eta^2 = 0.61$ , and a significant interaction,  $F(1, 21) = 8.54, p = 0.008, \eta^2 = 0.29$ . As shown in Figure 3E, in the early stage, the CDA amplitude of the dual-task condition ( $-1.41 \pm 0.21\mu\text{V}$ ) was similar to that in the single-task condition ( $-1.52 \pm 0.21\mu\text{V}$ ),  $t(21) = 1.01, p = 0.327$ , Cohen's  $d = 0.21$ , 95% CI =  $[-0.21, 0.63]$ . While in the late stage, the CDA amplitude under the dual-task condition ( $0.46 \pm 0.12\mu\text{V}$ ) significantly lower than the single-task condition ( $0.95 \pm 0.17\mu\text{V}$ ),  $t(21) = 2.82, p = 0.01$ , Cohen's  $d = 0.60$ , 95% CI =  $[0.14, 1.05]$ . Combined with impaired memory performance under the dual-task condition, this finding suggests that visual WM processing was already affected at the late retention stage after the onset of the secondary task.

Cluster-based permutation test was also used to further confirm these results. As shown in Figure 3A, the analysis revealed that for the single-task condition, there was a significant CDA both during the early (significant time points: 226-580 msec,  $p < 0.05$ , cluster corrected) and the late stage (significant time points: 606-1100 msec,  $p < 0.05$ , cluster corrected). While for the dual-task condition, the CDA during the early stage (significant time points: 228-582 msec,  $p < 0.05$ , cluster corrected) was not affected by the secondary task, but not the late stage (significant time points are compressed: 672-994 msec,  $p < 0.05$ , cluster corrected). Consistent with these results, the difference between the single- and dual-task conditions was mainly significant in the late stage (significant time points: 598-758 msec and 918-1100 msec,  $p < 0.05$ , cluster corrected).

<PLEASE INSERT FIGURE 3 HERE>

### 3.2.2. Alpha lateralization

We tested whether the impaired memory performance was due to the occupation of visuospatial attention by the secondary task. To this end, we use alpha lateralization to index the amount of visuospatial attention resources allocated to the lateralized memory representations.

As Figure 3B shows, we observed a typical alpha lateralization under the single-task condition, but not the dual-task condition, especially in the late stage. We verified this observation with a repeated measures ANOVA on alpha lateralization with the factors condition (single vs. dual-task) and retention stage (early vs. late). The analysis revealed a significant main effect of condition,  $F(1, 21) = 8.29, p = 0.009, \eta^2 = 0.28$ , but not the main effect of retention stage,  $F(1, 21) = 1.97, p = 0.175, \eta^2 = 0.09$ , and the interaction,  $F(1, 21) = 1.21, p = 0.284, \eta^2 = 0.05$ . This analysis seems to suggest that, the modulation of alpha lateralization by the secondary task showed the same pattern at both stages. However, as shown in Figure 3F, paired-samples  $t$  tests showed that in the early stage, alpha lateralization did not take shape in the single-task condition ( $-0.75 \pm 0.78\%$ ),  $t(21) = -0.957, p = 0.349$ , Cohen's  $d = -0.204$ , 95% CI =  $[-0.62, 0.22]$ , or the dual-task condition ( $0.55 \pm 0.59\%$ ),  $t(21) = 0.92, p = 0.368$ , Cohen's  $d = 0.19$ , 95% CI =  $[-0.23, 0.62]$ . While in the late stage, considerable alpha lateralization could be observed under the single-task condition ( $-1.81 \pm 0.60\%$ ),  $t(21) = 3.01, p = 0.007$ , Cohen's  $d = 0.64$ , 95% CI =  $[0.17, 1.1]$ , but still not the dual-task condition ( $0.24 \pm 0.65\%$ ),  $t(21) = 0.37, p = 0.731$ , Cohen's  $d = 0.08$ , 95% CI =  $[-0.34, 0.49]$ .

We further confirmed this impression by performing the cluster-based permutation test. As shown in Figure 3B, this analysis revealed that the alpha

lateralization had not yet taken shape during the early stage of both the single- and dual-task conditions, also with no difference between conditions. At the late stage however, a clear alpha lateralization appeared in the single-task condition (significant time points: 512-968 msec,  $p < 0.05$ , cluster corrected), but still not in the dual-task condition, resulting in a significant difference between the single- and dual-task conditions (significant time points: 548-1096 msec,  $p < 0.05$ , cluster corrected). The obvious alpha lateralization under the single-task condition, in which participants only needed to perform the visual WM task, is consistent with previous studies (de Vries et al., 2017; Myers et al., 2015; Sauseng et al., 2005; Thut et al., 2006), further confirming the robustness of this phenomenon. In contrast, alpha lateralization disappeared under the dual-task condition, meaning that the visuospatial attention guided to individual memory representations was successfully occupied by the secondary task.

### 3.3. Correlations between alpha lateralization, CDA and memory performance

Next, we assessed whether the extent to which visuospatial attention was occupied correlated with the maintenance-related neural activity and subsequent behavioral impairment in both retention stage. To this end, we took the corresponding values of alpha lateralization, CDA amplitude and behavior performance (K) of single-task condition minus the corresponding value of dual-task condition as the differentials, and then calculated the Pearson correlation coefficient between the three values. In the early stage, there was no significant correlation between alpha lateralization, CDA amplitude and the memory performance (all  $p > 0.172$ ). In contrast, during the late stage, alpha lateralization was significantly correlated with the contemporaneous CDA amplitude ( $r = 0.495$ ,  $p = 0.019$ ) and the behavioral performance ( $r = -0.532$ ,  $p = 0.011$ ) (see Figure 4A-B). Besides, the CDA amplitude of the late stage was also significantly correlated with the subsequent memory performance ( $r = -0.48$ ,  $p = 0.0243$ ) (see Figure

4C), but not the early stage ( $p = 0.145$ ). These evidences supported the notion that CDA is sensitive to the amount of information maintained in visual WM, and suggested that the accessibility of visuospatial attention resources during the maintenance stage affect the neural representation of working memory contents and the subsequent behavioral performance.

<PLEASE INSERT FIGURE 4 HERE>

#### 4. Discussion

In this study, we investigated the role of visuospatial attention for the maintenance of visual representations in working memory. By canceling the time interval between the offset of the secondary task and memory probe, the re-entry of visuospatial attention was prevented before the probe was presented. We were interested in how the disruption of visuospatial attention during the retention interval affected the real-time storage of visual WM and the neural oscillations associated with visuospatial attention. To this end, we divided the retention interval into two stages, the early stage and late stage, bounded by the onset of the secondary task. We found that the CDA amplitude was significantly reduced in the dual-task condition compared with the single-task condition, but only in the late stage and was associated with impaired memory performance. Consistent with the CDA modulations, with the execution of secondary task, alpha lateralization was significantly reduced, indicating the disruption of lateral-allocated visuospatial attention. More importantly, in the late stage, rather than the early stage, the degree of alpha lateralization reduction was significantly correlated with the degree of CDA reduction and impaired memory performance. These evidences directly proved that visual WM improves

when covert visuospatial attention is allowed to guide to individual memory representations.

An alternative explanation for impaired memory performance under the dual-task condition require discussion. Under this condition, main WM task and secondary task were set to be detected with equal probability, which made the probability of WM task being detected was only half of that under the single-task condition. Thus, the difference of detection probability between conditions might induce participants to adopt different strategies to perform the WM task. Specifically, in dual-task condition, participants might be inclined to give up encoding all sample arrays into WM in some trials due to the low detection probability. However, this explanation does not fit the current pattern of results. We found that the separation of CDA amplitudes between conditions occurred only at the late-stage (see Figure 3A), which means that the amount of information maintained in visual WM was comparable between conditions before the secondary task was presented. Not only that, the strategic perspective cannot explain the correlation between different indicators very well. Based on these considerations, it is difficult to believe that the current pattern of results was primarily due to the contribution of detection probability.

In the classic interpretation, the amplitude of CDA, which sustained throughout the delay period of visual WM task, reflects the number of items being held in visual WM. As supporting evidence, it has been shown that CDA amplitudes increase when memory load is increased (Vogel and Machizawa, 2004; for review see Luria et al., 2016), and varied with the fluctuations in memory performance (Adam et al., 2018). In current study, the basic observation is that CDA amplitude decreased with the disruption of visuospatial attention, and the two neurological indicators were closely related. According to the classic interpretation, this result pattern reflected the loss of

real-time stored information without the protection of sustained visuospatial attention. This explanation, however, may not be consistent with previous evidences. Work from multiple laboratories found that inserting attention task during the retention interval did not impair subsequent memory performance (Hollingworth and Maxcey-Richard, 2013; Maxcey-richard and Hollingworth, 2013; Rerko et al., 2014; Souza and Oberauer, 2017). Although this was based on behavioral evidence, it is inferred that in these studies, the disruption of visual spatial attention did not have an irreversible effect on the real-time storage of WM contents. We'll come back to this point later. Here, we consider another explanation, that the regulation of CDA amplitude between conditions might reflect when visuospatial attention was disrupted, part of the visual WM contents was temporarily shifted to the silent state. This is in view of the idea that WM contents can be stored out of the focus of attention, as the state-based theories suggested (Cowan, 1995; McElree, 1996; Oberauer, 2002; for review see Larocque et al., 2014), and that the representation states of information within WM are highly flexible (Rose et al., 2016; Wolff et al., 2015, 2017; Zokaei et al., 2014). In fact, as a macroscopic measure of sustained neuronal firing, CDA may reflect the tracking of active neural representations, which are only present for WM contents currently in the focus of attention (Berggren and Eimer, 2016). Consistent with this view, researchers have found that active neural representations of memory item outside the focus of attention (i.e., silent state) are not evident in CDA amplitude. For example, in a visual search task, Carlisle et al. (2011) found that with each successive trial searching for the same target, the CDA magnitude induced by the search template decreased, reflecting that search template was unloaded out of the focus of attention. In a recent work, Göddertz and colleagues guided the subjects to selectively maintain an item in the focus of attention by presenting retro-cue during the delay interval of visual WM task (Göddertz et al., 2018). They found that, when looking at separate performance quantiles (bad, medium, vs. good performance), a CDA was only present in good performance trials, suggesting that it is an optional

mechanism that facilitates active retention of the cued item in the focus of attention. Theoretically, if WM contents are maintained by alternative mechanisms besides one relying on sustained neural firing, such as through the activity-silent synaptic mechanisms (Mongillo et al., 2008; Stokes, 2015), then no CDA amplitude above the baseline will be generated. This was particularly possible in the present study, consider the steady finding that the active neural representation of WM item would not be detectable in BOLD or EEG signal when internal attention is diverted from it (LaRocque et al., 2013; Lewis-Peacock et al., 2012; Wolff et al., 2015, 2017). However, our other results showed that this operation (if occurred) did not reverse the subsequent deterioration in behavior performance. Memory performance was significantly impaired under the dual-task condition. One possible explanation is that offloading memory items to the silent state might be detrimental to maintaining them. However, previous evidences do not seem to support this view. In a color-in-location recognition task with the state of the WM representations being prioritized by retro-cue, Rerko and Oberauer (2013) directly compared the memory performance for items maintained in (i.e., active state) and out of the focus of attention (i.e., silent state). Their results have shown no drop in performance for unattended memory items, compared with items maintained in the focus of attention. Further evidence came from a recent study by Wolff et al. (2017). They developed a perturbation approach to measure the reactivated activity patterns of memoranda in different states. The main finding was that memory-item-specific activity was decodable from the impulse response, both in active state and silent state. Besides, trial-wise variability of silent-state coding predicted variability in subsequent WM performance. Therefore, one of the important aspects of their evidence revealed is that, if the information was successfully maintained in WM, there would be a corresponding neural trace, irrespective of representation state. Overall, these evidences showed that WM contents can also be offloaded into the silent state for short-term storage.

Next, we discuss the mechanisms that might lead to impaired memory performance during the detection stage. As mentioned in the introduction section, in those studies that failed to observe the adverse effects of disrupting visuospatial attention during delay interval, attention was allowed to return after the execution of secondary task. In contrast, the current design continued to occupy visuospatial attention that guided to lateralized memory representations until the probe was onset. This setting made it difficult to retrieve memory items into the focus of attention before the probe arrived. In fact, participants could also activate the silent state representations during the detection stage. This seemed to be feasible, but might face failure. Because memory probe could disrupt, bias, or replace the vulnerable memory representations, especially because probe and memoranda shared same features, therefore may utilize the same neural substrate (Makovski et al., 2008; Makovski et al., 2010). By contrast, loading memory items into the active state before probe arrived was beneficial, considering that memory representations in the active state are more accessible (Cowan, 1995; Oberauer, 2002), which makes it possible to refresh them (Barrouillet and Portrat, 2011; Vergauwe and Cowan, 2015). Notably, some recent researchers found that using retroactive cues to select WM item in the focus of attention helps to resist interference from perceptual inputs that share the same feature (Barth and Schneider, 2018; van Moorselaar et al., 2015). Unfortunately, these studies did not examine whether items outside the focus of attention were similarly protected. Furthermore, memoranda in the active state was proved to be easier to interact with inputting perceptual information than items in the silent state (Bahle et al., 2018; Beck et al., 2012; Hollingworth and Beck, 2016; Olivers et al., 2011). This mechanism is useful for sensitive detection of whether the perceptual input (i.e., memory probe) matches the WM contents at test. Therefore, it is reasonable to believe that pre-retrieving memory items into the focus of attention before the detection stage can facilitate subsequent WM performance. In any case, the evidence presented in current study confirmed that even beyond the initial



encoding stage, the visual WM system still needs the participation of visuospatial attention to work well. We suggest more researches in the future explore the participation mechanism of visuospatial attention in WM processing.

The present findings contribute to a growing body of evidences that the same visuospatial attention mechanism operates in the perceptual scenes and visual WM (Kiyonaga and Egnér, 2013; Sahan et al., 2016). First, it has been observed that attention to visibly present stimuli and visibly absent memory representations follow the same principle, and modulates the visual cortex retinotopically in a similar way. In the perceptual scene, the modulation of attention can be space-based, enhancing activity to attended stimulus and suppressing neural responses when visuospatial attention was directed elsewhere (Gandhi et al., 1999; Somers et al., 1999). It can also operate in an object-based manner. The perceptual grouping of the shifting target feature could modulate the BOLD signals associated with attentional shifting in retinotopic areas (Müller and Kleinschmidt, 2003; Shomstein and Behrmann, 2006). Similarly, in the internal representation space, shifting attention within WM representations also activates the early visual cortex in a retinotopic fashion (Munneke et al., 2012). Besides, directing visual attention to one location that constitutes a single object held in WM also enhanced visuotopic activity in visual cortex for other positions on the same object (Peters et al., 2015), suggesting that attentional selection in visual WM can also operate in an object-based manner. Second, some cognitive phenomena previously thought to be unique to visuospatial attention processing, such as the inhibition-of return (Johnson et al., 2013), surround suppression (Kiyonaga and Egnér, 2016), crowding (Tamber-Rosenau et al., 2015), and Ponzo illusion (Shen et al., 2015), have also been observed in visual WM processing. Infact, maintaining a unified visuospatial attention system has its strong

practical significance, considering that it promotes frequent information interaction between internal memory representations and perceptual inputs. It should be noted, however, that it is difficult to agree with the view that visual WM and visual attention belong to a same selection mechanism with limited capacity, or different aspects of the same thing. There should be a mechanism that allows the short-term storage of visual information to operate independently of visuospatial attention in some cases. In the jungle, for example, hunters are perfectly capable of selectively remembering newly discovered prey while shifting their eyes to the quiver behind them. The multi-state theory framework of WM perfectly adapts to this demand. According to previous evidences, when attention is shifted elsewhere, items can also be effectively maintained by offloading them into the silent state, or using visual long-term memory (Cowan, 1995; Lewis-Peacock and Postle, 2008). While the “working” function of the visual WM system may only be supported by the state of high accessibility. The findings presented here suggest that the unified visuospatial attention system may play a key role in maintaining visual representation in the active state.

In summary, the current study showed that visual WM processing improves when sustained visuospatial attention is available during the retention stage. By preventing the return of visuospatial attention before the detection stage, we provided the first electrophysiological evidence that continuous disruption of the visuospatial attention is detrimental to visual WM process. We observed that greater reduction of alpha lateralization indicating a more disruption of visuospatial attention was associated with greater reduction of maintenance-related neural activity and larger impairment of behavioral performance. These findings improve our understanding of how visual WM

system works and further confirmed the close relationship between visual WM and visuospatial attention.

### **Acknowledgments**

The study was supported by grants from the National Natural Science Foundation of China (NSFC 31571123) to QL. TL QL completed the analysis and drafted the manuscript. All authors plan Experiment and modified the manuscript.

### **Disclosure of interest**

The authors report no conflicts of interest.

### **References**

- Adam, K.C.S., Robison, M.K., Vogel, E.K., 2018. Contralateral delay activity tracks fluctuations in working memory performance. *J. Cogn. Neurosci.* 30, 1229–1240. [https://doi.org/10.1162/jocn\\_a\\_01233](https://doi.org/10.1162/jocn_a_01233)
- Albers, A.M., Kok, P., Toni, I., Dijkerman, H.C., de Lange, F.P., 2013. Shared representations for working memory and mental imagery in early visual cortex. *Curr. Biol.* 23, 1427–1431. <https://doi.org/10.1016/j.cub.2013.05.065>
- Bahle, B., Beck, V.M., Hollingworth, A., 2018. The architecture of interaction between visual working memory and visual attention. *J. Exp. Psychol. Hum. Percept. Perform.* 44, 992–1011. <https://doi.org/10.1037/xhp0000509>
- Barrouillet, P., Portrat, S., 2011. On the law relating processing to storage in working memory. *Psychol. Rev.* 118, 175–192. <https://doi.org/10.1037/a0022324>

- Barth, A., Schneider, D., 2018. Manipulating the focus of attention in working memory: Evidence for a protection of multiple items against perceptual interference. *Psychophysiology* 55, e13062. <https://doi.org/10.1111/psyp.13062>
- Bays, P.M., 2014. Noise in Neural Populations Accounts for Errors in Working Memory. *J. Neurosci.* 34, 3632–3645. <https://doi.org/10.1523/JNEUROSCI.3204-13.2014>
- Beck, V.M., Hollingworth, A., Luck, S.J., 2012. Simultaneous Control of Attention by Multiple Working Memory Representations. *Psychol. Sci.* 23, 887–898. <https://doi.org/10.1007/s00253-017-8245-1>
- Belopolsky, A. V., Kramer, A.F., Godijn, R., 2008. Transfer of information into working memory during attentional capture. *Vis. cogn.* 16, 409–418. <https://doi.org/10.1080/13506280701695454>
- Berggren, N., Eimer, M., 2016. Does Contralateral Delay Activity Reflect Working Memory Storage or the Current Focus of Spatial Attention within Visual Working Memory? *J. Cogn. Neurosci.* 28, 2003–2020. [https://doi.org/10.1162/jocn\\_a\\_01019](https://doi.org/10.1162/jocn_a_01019)
- Brefczynski, J.A., DeYoe, E.A., 1999. A physiological correlate of the “spotlight” of visual attention. *Nat. Neurosci.* 2, 370–374. <https://doi.org/10.1038/7280>
- Carlisle, N.B., Arita, J.T., Pardo, D., Woodman, G.F., 2011. Attentional Templates in Visual Working Memory. *J. Neurosci.* 31, 9315–9322. <https://doi.org/10.1523/JNEUROSCI.1097-11.2011>
- Christophel, T.B., Iamshchinina, P., Yan, C., Allefeld, C., Haynes, J.D., 2018. Cortical specialization for attended versus unattended working memory. *Nat. Neurosci.* 21, 494–496. <https://doi.org/10.1038/s41593-018-0094-4>
- Clapp, W.C., Rubens, M.T., Gazzaley, A., 2010. Mechanisms of working memory disruption by external interference. *Cereb. Cortex* 20, 859–872. <https://doi.org/10.1093/cercor/bhp150>

- Cohen, J., 1977. *Statistical power analysis for the behavioral sciences* (rev. ed.).
- Cowan, N., 2001. The magical number 4 in short-term memory: A reconsideration of mental storage capacity. *Behav. Brain Sci.* 24, 87–114.  
<https://doi.org/10.1017/S0140525X01003922>
- Cowan, N., 1995. *Attention and Memory: An Integrated Framework*. Oxford: Oxford University Press.
- Cumming, G., Fidler, F., 2009. Confidence intervals better answers to better questions. *J. Psychol.* 217, 15–26. <https://doi.org/10.1027/0044-3409.217.1.15>
- de Vries, I.E.J., van Driel, J., Olivers, C.N.L., 2017. Posterior  $\alpha$  EEG Dynamics Dissociate Current from Future Goals in Working Memory-Guided Visual Search. *J. Neurosci.* 37, 1591–1603. <https://doi.org/10.1523/jneurosci.2945-16.2016>
- Delorme, A., Makeig, S., 2004. EEGLAB: An open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. *J. Neurosci. Methods* 134, 9–21. <https://doi.org/10.1016/j.jneumeth.2003.10.009>
- Emrich, S.M., Lockhart, H.A., Al-Aidroos, N., 2017. Attention mediates the flexible allocation of visual working memory resources. *J. Exp. Psychol. Hum. Percept. Perform.* 43, 1454–1465. <https://doi.org/10.1037/xhp0000398>
- Emrich, S.M., Riggall, A.C., LaRocque, J.J., Postle, B.R., 2013. Distributed Patterns of Activity in Sensory Cortex Reflect the Precision of Multiple Items Maintained in Visual Short-Term Memory. *J. Neurosci.* 33, 6516–6523.  
<https://doi.org/10.1523/JNEUROSCI.5732-12.2013>
- Ester, E.F., Anderson, D.E., Serences, J.T., Awh, E., 2013. A neural measure of precision in visual working memory. *J. Cogn. Neurosci.* 25, 754–761.  
[https://doi.org/10.1162/jocn\\_a\\_00357](https://doi.org/10.1162/jocn_a_00357)

- Feldmann-Wüstefeld, T., Vogel, E.K., Awh, E., 2018. Contralateral Delay Activity Indexes Working Memory Storage, Not the Current Focus of Spatial Attention. *J. Cogn. Neurosci.* 30, 1185–1196. [https://doi.org/10.1162/jocn\\_a\\_01271](https://doi.org/10.1162/jocn_a_01271)
- Gandhi, S.P., Heeger, D.J., Boynton, G.M., 1999. Spatial attention affects brain activity in human primary. *Proc. Natl. Acad. Sci.* 96, 3314–3319. <https://doi.org/10.1073/pnas.96.6.3314>
- Gayet, S., Paffen, C.L.E., Van der Stigchel, S., 2017. Visual Working Memory Storage Recruits Sensory Processing Areas. *Trends Cogn. Sci.* 22, 189–190. <https://doi.org/10.1016/j.tics.2017.09.011>
- Göddertz, A., Klatt, L.-I., Mertes, C., Schneider, D., 2018. Retroactive Attentional Shifts Predict Performance in a Working Memory Task: Evidence by Lateralized EEG Patterns. *Front. Hum. Neurosci.* 12, 1–14. <https://doi.org/10.3389/fnhum.2018.00428>
- Gressmann, M., Janczyk, M., 2016. The (Un)clear effects of invalid retro-cues. *Front. Psychol.* 7, 1–12. <https://doi.org/10.3389/fpsyg.2016.00244>
- Harrison, S.A., Tong, F., 2009. Decoding reveals the contents of visual working memory in early visual areas. *Nature* 458, 632–635. <https://doi.org/10.1038/nature07832>
- Hollingworth, A., Beck, V.M., 2016. Memory-based attention capture when multiple items are maintained in visual working memory. *J. Exp. Psychol. Hum. Percept. Perform.* 42, 911–917. <https://doi.org/10.1037/xhp0000230>
- Hollingworth, A., Maxcey-Richard, A.M., 2013. Selective maintenance in visual working memory does not require sustained visual attention. *J. Exp. Psychol. Hum. Percept. Perform.* 39, 1047–1058. <https://doi.org/10.1037/a0030238>
- Ikkai, A., Dandekar, S., Curtis, C.E., 2016. Lateralization in Alpha-Band Oscillations Predicts the Locus and Spatial Distribution of Attention. *PLoS One* 11, e0154796. <https://doi.org/10.1371/journal.pone.0154796>

- Infanti, E., Hickey, C., Turatto, M., 2015. Reward associations impact both iconic and visual working memory. *Vision Res.* 107, 22–29.  
<https://doi.org/10.1016/j.visres.2014.11.008>
- Itskov, V., Hansel, D., Tsodyks, M., 2011. Short-Term Facilitation may Stabilize Parametric Working Memory Trace. *Front. Comput. Neurosci.* 5, 1–19.  
<https://doi.org/10.3389/fncom.2011.00040>
- Johnson, M.R., Higgins, J.A., Norman, K.A., Sederberg, P.B., Smith, T.A., Johnson, M.K., 2013. Foraging for thought: an inhibition-of-return-like effect resulting from directing attention within working memory. *Psychol. Sci.* 24, 1104–1112.  
<https://doi.org/10.1177/0956797612466414>
- Johnston, J.C., McCann, R.S., Remington, R.W., 1995. Chronometric evidence for two types of attention. *Psychol. Sci.* 6, 365–369. <https://doi.org/10.1111/j.1467-9280.1995.tb00527.x>
- Kiyonaga, A., Egner, T., 2016. Center-Surround Inhibition in Working Memory. *Curr. Biol.* 26, 64–68. <https://doi.org/10.1016/j.cub.2015.11.013>
- Kiyonaga, A., Egner, T., 2013. Working memory as internal attention: Toward an integrative account of internal and external selection processes. *Psychon. Bull. Rev.* 20, 228–242. <https://doi.org/10.3758/s13423-012-0359-y>
- Klatt, L.I., Getzmann, S., Wascher, E., Schneider, D., 2018. Searching for auditory targets in external space and in working memory: Electrophysiological mechanisms underlying perceptual and retroactive spatial attention. *Behav. Brain Res.* 353, 98–107.  
<https://doi.org/10.1016/j.bbr.2018.06.022>
- Kronland-Martinet, R., Morlet, J., Grossmann, A., 1987. Analysis of Sound Patterns Through Wavelet Transforms, *International Journal of Pattern Recognition and Artificial Intelligence.* <https://doi.org/10.1142/S0218001487000205>

- LaRocque, J.J., Lewis-Peacock, J.A., Drysdale, A.T., Oberauer, K., Postle, B.R., 2013. Decoding attended information in short-term memory: An EEG study. *J. Cogn. Neurosci.* 25, 127–142. [https://doi.org/10.1162/jocn\\_a\\_00305](https://doi.org/10.1162/jocn_a_00305)
- Larocque, J.J., Lewis-peacock, J.A., Postle, B.R., 2014. Multiple neural states of representation in short-term memory? It's a matter of attention. *Front. Hum. Neurosci.* 8, 1–14. <https://doi.org/10.3389/fnhum.2014.00005>
- LaRocque, J.J., Riggall, A.C., Emrich, S.M., Postle, B.R., 2017. Within-Category Decoding of Information in Different Attentional States in Short-Term Memory. *Cereb. Cortex* 27, 4881–4890. <https://doi.org/10.1093/cercor/bhw283>
- Lewis-Peacock, J.A., Drysdale, A.T., Oberauer, K., Postle, B.R., 2012. Neural Evidence for a Distinction between Short-term Memory and the Focus of Attention. *J. Cogn. Neurosci.* 24, 61–79. [https://doi.org/10.1162/jocn\\_a\\_00140](https://doi.org/10.1162/jocn_a_00140)
- Lewis-Peacock, J.A., Postle, B.R., 2008. Temporary Activation of Long-Term Memory Supports Working Memory. *J. Neurosci.* 28, 8765–8771. <https://doi.org/10.1523/JNEUROSCI.1953-08.2008>
- Luria, R., Balaban, H., Awh, E., Vogel, E.K., 2016. The contralateral delay activity as a neural measure of visual working memory. *Neurosci. Biobehav. Rev.* 62, 100–108. <https://doi.org/10.1016/j.neubiorev.2016.01.003>
- Makovski, T., Sussman, R., Jiang, Y. V., 2008. Orienting Attention in Visual Working Memory Reduces Interference From Memory Probes. *J. Exp. Psychol. Learn. Mem. Cogn.* 34, 369–380. <https://doi.org/10.1037/0278-7393.34.2.369>
- Makovski, T., Watson, L.M., Koutstaal, W., Jiang, Y. V., 2010. Method matters: systematic effects of testing procedure on visual working memory sensitivity. *J. Exp. Psychol. Learn. Mem. Cogn.* 36, 1466–1479. <https://doi.org/10.1037/a0020851>



- Maris, E., Oostenveld, R., 2007. Nonparametric statistical testing of EEG-and MEG-data. *J. Neurosci. Methods* 164, 177–190. <https://doi.org/10.1016/j.jneumeth.2007.03.024>
- Marsman, M., Wagenmakers, E.J., 2017. Bayesian benefits with JASP. *Eur. J. Dev. Psychol.* 14, 545–555. <https://doi.org/10.1080/17405629.2016.1259614>
- Maxcey-richard, A.M., Hollingworth, A., 2013. The Strategic Retention of Task-Relevant Objects in Visual Working Memory. *J. Exp. Psychol. Learn. Mem. Cogn.* 39, 760–772. <https://doi.org/10.1037/a0029496>
- McElree, B., 1996. Accessing short-term memory with semantic and phonological information: A time-course analysis. *Mem. Cogn.* 24, 173–187. <https://doi.org/10.3758/BF03200879>
- Mongillo, G., Barak, O., Tsodyks, M., 2008. Synaptic theory of working memory. *Science* (80-. ). 319, 1543–1546. <https://doi.org/10.1126/science.1150769>
- Müller, N.G., Kleinschmidt, A., 2003. Dynamic Interaction of Object- and Space-Based Attention in Retinotopic Visual Areas. *J. Neurosci.* 23, 9812–9816.
- Munneke, J., Belopolsky, A. V, Theeuwes, J., 2012. Shifting Attention within Memory Representations Involves Early Visual Areas. *PLoS One* 7. <https://doi.org/10.1371/journal.pone.0035528>
- Myers, N.E., Walther, L., Wallis, G., Stokes, M.G., Nobre, A.C., 2015. Temporal dynamics of attention during encoding vs. maintenance of working memory: complementary views from event-related potentials and alpha-band oscillations. *J. Cogn. Neurosci.* 27, 492–508. [https://doi.org/10.1162/jocn\\_a\\_00727](https://doi.org/10.1162/jocn_a_00727)
- Nee, D.E., Jonides, J., 2013. Neural evidence for a 3-state model of visual short-term memory. *Neuroimage* 74, 1–11. <https://doi.org/10.1016/j.neuroimage.2013.02.019>

- Oberauer, K., 2002. Access to Information in Working Memory: Exploring the Focus of Attention. *J. Exp. Psychol. Learn. Mem. Cogn.* 28, 411–421.  
<https://doi.org/10.1037/0278-7393.28.3.411>
- Olivers, C.N.L., Peters, J., Houtkamp, R., Roelfsema, P.R., 2011. Different states in visual working memory: When it guides attention and when it does not. *Trends Cogn. Sci.* 15, 327–334. <https://doi.org/10.1016/j.tics.2011.05.004>
- Pasternak, T., Greenlee, M.W., 2005. Working memory in primate sensory systems. *Nat. Rev. Neurosci.* 6, 97–107. <https://doi.org/10.1038/nrn1603>
- Pertsov, Y., Bays, P.M., Joseph, S., Husain, M., 2012. Rapid Forgetting Prevented by Retrospective Attention Cues. *J. Exp. Psychol. Hum. Percept. Perform.* 39, 1224–1231. <https://doi.org/10.1037/a0030947>
- Peters, B., Kaiser, J., Rahm, B., Bledowski, C., 2015. Activity in Human Visual and Parietal Cortex Reveals Object-Based Attention in Working Memory. *J. Neurosci.* 35, 3360–3369. <https://doi.org/10.1523/JNEUROSCI.3795-14.2015>
- Poch, C., Capilla, A., Hinojosa, J.A., Campo, P., 2017. Selection within working memory based on a color retro-cue modulates alpha oscillations. *Neuropsychologia* 106, 133–137. <https://doi.org/10.1016/j.neuropsychologia.2017.09.027>
- Poch, C., Valdivia, M., Capilla, A., Hinojosa, J.A., Campo, P., 2018. Suppression of no-longer relevant information in Working Memory: An alpha-power related mechanism? *Biol. Psychol.* 135, 112–116. <https://doi.org/10.1016/j.biopsycho.2018.03.009>
- Posner, M.I., 1980. Orienting of attention. *Q. J. Exp. Psychol.* 32, 3–25.
- Posner, Michael I, Petersen, S.E., 1990. The Attention Systems of the Human Brain. *Annu. Rev. Neurosci.* 13, 25–42. [https://doi.org/10.1007/978-1-4471-5649-9\\_1](https://doi.org/10.1007/978-1-4471-5649-9_1)
- Posner, M. I., Petersen, S.E., 1990. The attention system of the human brain. *Annu. Rev. Neurosci.* 13, 25–42. <https://doi.org/10.1146/annurev.ne.13.030190.000325>

- Rerko, L., Oberauer, K., 2013. Focused, unfocused, and defocused information in working memory. *J. Exp. Psychol. Learn. Mem. Cogn.* 39, 1075–1096.  
<https://doi.org/10.1037/a0031172>
- Rerko, L., Souza, A.S., Oberauer, K., 2014. Retro-cue benefits in working memory without sustained focal attention. *Mem. Cogn.* 42, 712–728. <https://doi.org/10.3758/s13421-013-0392-8>
- Rose, N.S., LaRocque, J.J., Riggall, A.C., Gosseries, O., Starrett, M.J., Meyering, E.E., Postle, B.R., 2016. Reactivation of latent working memories with transcranial magnetic stimulation. *Science (80-. )*. 354, 1136–1139. <https://doi.org/10.1126/science.aah7011>
- Sahan, M.I., Verguts, T., Boehler, C.N., Pourtois, G., Fias, W., 2016. Paying attention to working memory: Similarities in the spatial distribution of attention in mental and physical space. *Psychon. Bull. Rev.* 23, 1190–1197. <https://doi.org/10.3758/s13423-015-0990-5>
- Sauseng, P., Klimesch, W., Stadler, W., Schabus, M., Doppelmayr, M., Hanslmayr, S., Gruber, W.R., Birbaumer, N., 2005. A shift of visual spatial attention is selectively associated with human EEG alpha activity. *Eur. J. Neurosci.* 22, 2917–2926.  
<https://doi.org/10.1111/j.1460-9568.2005.04482.x>
- Schmidt, B.K., Vogel, E.K., Woodman, G.F., Luck, S.J., 2002. Voluntary and automatic attentional control of visual working memory. *Percept. Psychophys.* 64, 754–763.  
<https://doi.org/10.3758/bf03194742>
- Schmidt, T.T., Blankenburg, F., 2018. Brain regions that retain the spatial layout of tactile stimuli during working memory- A ‘tactospacial sketchpad’? *Neuroimage* 178, 531–539. <https://doi.org/10.1016/j.neuroimage.2018.05.076>

- Schmidt, T.T., Ostwald, D., Blankenburg, F., 2014. Imaging tactile imagery: Changes in brain connectivity support perceptual grounding of mental images in primary sensory cortices. *Neuroimage* 98, 216–224. <https://doi.org/10.1016/j.neuroimage.2014.05.014>
- Serences, J.T., Ester, E.F., Vogel, E.K., Awh, E., 2009. Stimulus-specific delay activity in human primary visual cortex. *Psychol. Sci.* 20, 207–214. <https://doi.org/10.1111/j.1467-9280.2009.02276.x>
- Shen, M., Xu, H., Zhang, H., Shui, R., Zhang, M., Zhou, J., 2015. The working memory Ponzo illusion: Involuntary integration of visuospatial information stored in visual working memory. *Cognition* 141, 26–35. <https://doi.org/10.1016/j.cognition.2015.04.010>
- Shomstein, S., Behrmann, M., 2006. Cortical systems mediating visual attention to both objects and spatial locations. *Proc. Natl. Acad. Sci. U. S. A.* 103, 11387–11392. <https://doi.org/10.1073/pnas.0601813103>
- Sneve, M.H., Alnæs, D., Endestad, T., Greenlee, M.W., Magnussen, S., 2012. Visual short-term memory : Activity supporting encoding and maintenance in retinotopic visual cortex. *Neuroimage* 63, 166–178. <https://doi.org/10.1016/j.neuroimage.2012.06.053>
- Somers, D.C., Dale, A.M., Seiffert, A.E., Tootell, R.B.H., 1999. Functional MRI reveals spatially specific attentional modulation in human primary visual cortex. *Proc. Natl. Acad. Sci.* 96, 1663–1668. <https://doi.org/10.1073/pnas.96.4.1663>
- Souza, A.S., Oberauer, K., 2017. The contributions of visual and central attention to visual working memory. *Attention, Perception, Psychophys.* 79, 1897–1916. <https://doi.org/10.3758/s13414-017-1357-y>
- Sreenivasan, K.K., Vytlačil, J., D’Esposito, M., 2014. Distributed and dynamic storage of working memory stimulus information in extrastriate cortex. *J. Cogn. Neurosci.* 26, 1141–1153. [https://doi.org/10.1162/jocn\\_a\\_00556](https://doi.org/10.1162/jocn_a_00556)

- Stokes, M.G., 2015. “Activity-silent” working memory in prefrontal cortex: A dynamic coding framework. *Trends Cogn. Sci.* 19, 394–405.  
<https://doi.org/10.1016/j.tics.2015.05.004>
- Stokes, M.G., Kusunoki, M., Sigala, N., Nili, H., Gaffan, D., Duncan, J., 2013. Dynamic coding for cognitive control in prefrontal cortex. *Neuron* 78, 364–375.  
<https://doi.org/10.1016/j.neuron.2013.01.039>
- Tamber-Rosenau, B.J., Fintzi, A.R., Marois, R., 2015. Crowding in visual working memory reveals its spatial resolution and the nature of its representations. *Psychol. Sci.* 26, 1511–1521. <https://doi.org/10.1177/0956797615592394>
- Tanoue, R.T., Berryhill, M.E., 2012. The mental wormhole : Internal attention shifts without regard for distance. *Attention, Perception, Psychophys.* 74, 1199–1215.  
<https://doi.org/10.3758/s13414-012-0305-0>
- Thut, G., Nietzel, A., Brandt, S.A., Pascual-Leone, A., 2006. Alpha-band electroencephalographic activity over occipital cortex indexes visuospatial attention bias and predicts visual target detection. *J. Neurosci.* 26, 9494–9502.  
<https://doi.org/10.1523/JNEUROSCI.0875-06.2006>
- Tsubomi, H., Fukuda, K., Watanabe, K., Vogel, E.K., 2013. Neural Limits to Representing Objects Still within View. *J. Neurosci.* 33, 8257–8263.  
<https://doi.org/10.1523/JNEUROSCI.5348-12.2013>
- van Moorselaar, D., Gansel, E., Theeuwes, J., N L Olivers, C., 2015. The time course of protecting a visual memory representation from perceptual interference. *Front. Hum. Neurosci.* 8, 1053. <https://doi.org/10.3389/fnhum.2014.01053>
- Vergauwe, E., Cowan, N., 2015. Attending to items in working memory: evidence that refreshing and memory search are closely related. *Psychon. Bull. Rev.* 22, 1001–1006.  
<https://doi.org/10.3758/s13423-014-0755-6>

- Vogel, E. K., Machizawa, M.G., 2004. Neural activity predicts individual differences in visual working memory capacity. *Nature* 428, 748–751.  
<https://doi.org/10.1038/nature02447>
- Vogel, Edward K., Machizawa, M.G., 2004. Neural activity predicts individual differences in visual working memory capacity. *Nature* 428, 748–751.  
<https://doi.org/10.1038/nature02447>
- Wang, F., Chen, M., Yan, Y., Zhaoping, L., Li, W., 2015. Modulation of Neuronal Responses by Exogenous Attention in Macaque Primary Visual Cortex. *J. Neurosci.* 35, 13419–13429. <https://doi.org/10.1523/JNEUROSCI.0527-15.2015>
- Williams, M., Pouget, P., Boucher, L., Woodman, G.F., 2013. Visual–spatial attention aids the maintenance of object representations in visual working memory. *Mem. Cognit.* 41, 698–715. <https://doi.org/10.3758/s13421-013-0296-7>
- Wolff, M.J., Ding, J., Myers, N.E., Stokes, M.G., 2015. Revealing hidden states in visual working memory using electroencephalography. *Front. Syst. Neurosci.* 9.  
<https://doi.org/10.3389/fnsys.2015.00123>
- Wolff, M.J., Jochim, J., Akyürek, E.G., Stokes, M.G., 2017. Dynamic hidden states underlying working-memory-guided behavior. *Nat. Neurosci.* 20, 864–871.  
<https://doi.org/10.1038/nn.4546>
- Woodman, G.F., Vogel, E.K., 2005. Fractionating working memory: consolidation and maintenance are independent processes. *Psychol. Sci.* 16, 106–113.  
<https://doi.org/10.2307/40064186>
- Woodman, G.F., Vogel, E.K., Luck, S.J., 2001. Visual Search Remains Efficient When Visual Working Memory Is Full. *Psychol. Sci.* 12, 219–224.  
<https://doi.org/10.2307/40063582>

- Worden, M.S., Foxe, J.J., Wang, N., Simpson, G. V, 2000. Anticipatory biasing of visuospatial attention indexed by retinotopically specific alpha-band electroencephalography increases over occipital cortex. *J. Neurosci.* 20, 1–6. [https://doi.org/10.1016/S0165-3806\(00\)00002-X](https://doi.org/10.1016/S0165-3806(00)00002-X)
- Xie, W., Zhang, W., 2017. Familiarity speeds up visual short-term memory consolidation: electrophysiological evidence from contralateral delay activities. *J. Cogn. Neurosci.* 30, 1–13. [https://doi.org/10.1162/jocn\\_a\\_01188](https://doi.org/10.1162/jocn_a_01188)
- Zokaei, N., Manohar, S., Husain, M., Feredoes, E., 2014. Causal Evidence for a Privileged Working Memory State in Early Visual Cortex. *J. Neurosci.* 34, 158–162. <https://doi.org/10.1523/JNEUROSCI.2899-13.2014>
- Zokaei, Nahid, Ning, S., Manohar, S., Feredoes, E., Husain, M., 2014. Flexibility of representational states in working memory. *Front. Hum. Neurosci.* 8. <https://doi.org/10.3389/fnhum.2014.00853>

## Figures

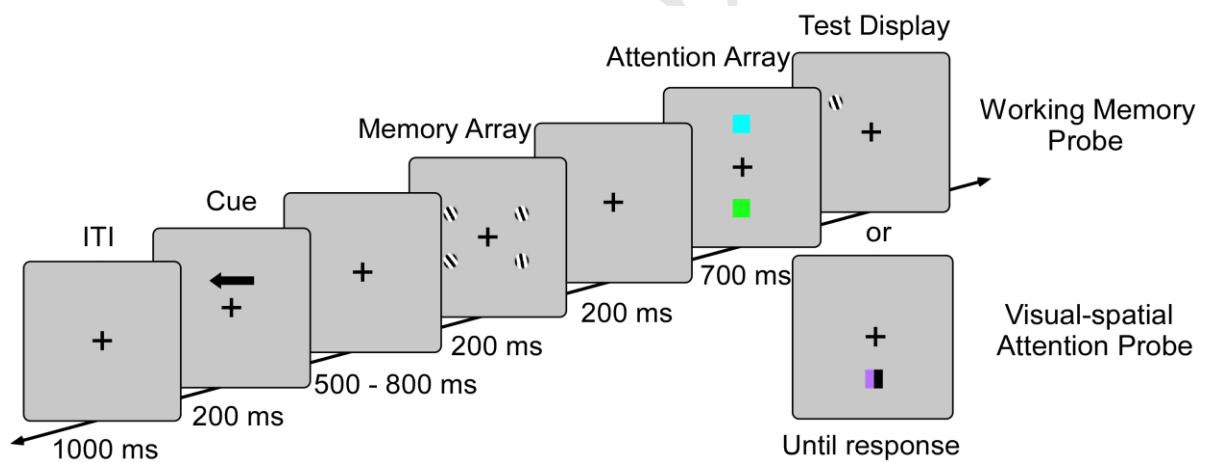


Figure 1. Schematic representation of the dual-task trials. Example working memory test display shows a no-change trial, and example attention detection display shows a change trial. Under the dual-task blocks, the probability of occurrence of the two detection cases was the same. While under the baseline-task blocks, only the working memory test display was presented, and the participants were told in advance to ignore the persistently visible stimuli presented on the central axis. See the online article for the color version of this figure.



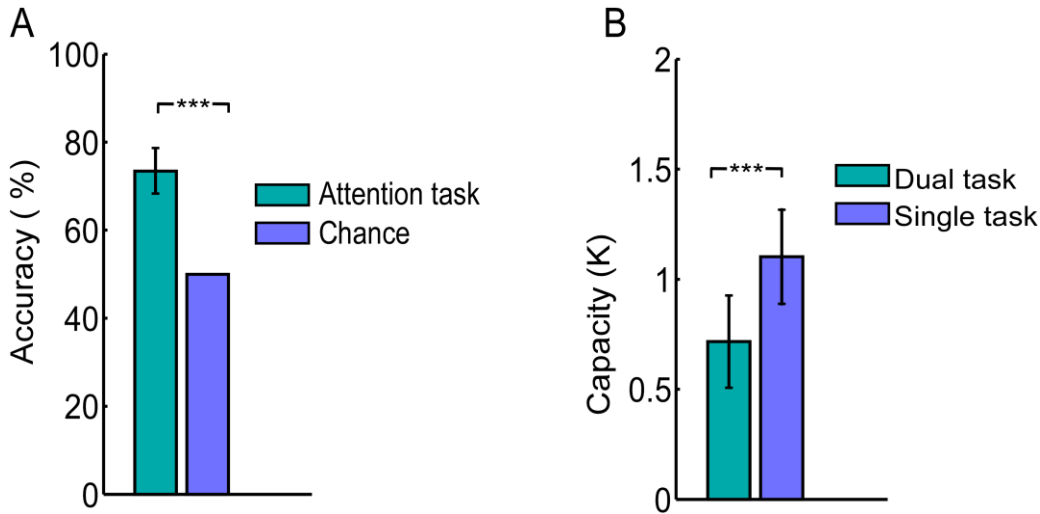


Figure 2. Behavioral performance. (A) Average accuracy in the attention task, compared with the chance level. (B) Average K score in the WM task for each condition. Error bars represent standard errors of the means. (\*\*\*) $p < 0.001$ .

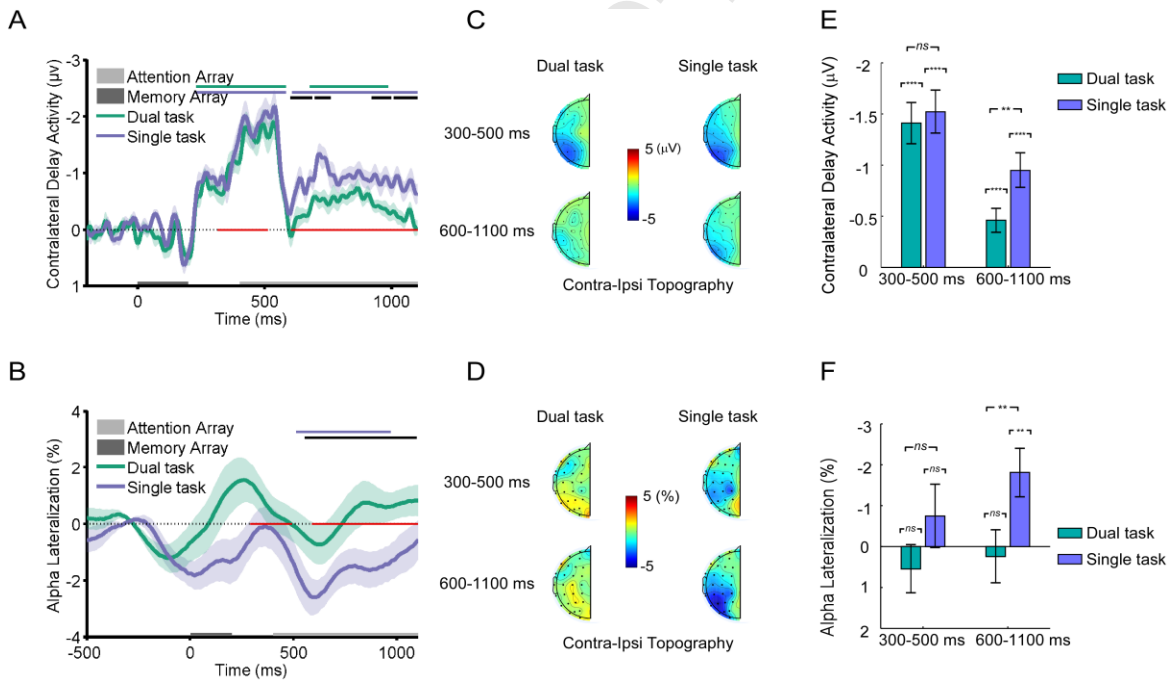


Figure 3. Contralateral delay activity (A) and alpha lateralization (B) over time for both dual- and single-task conditions. Time point zero marks the onset of the memory array, and time point 1100 marks the onset of the detection display. The red line indicates the time window of interest (300-500 msec and 600-1100 msec). Different colored lines along the top of CDA plot and alpha lateralization plot mark the data points at which either the difference of both neural indicators between dual- and single-task conditions (black) or the neural indicators itself for each condition (green for dual-task condition and purple for single-task condition) were significantly different than zero (permutation test,  $n = 22$ , cluster-defining threshold  $p < 0.05$ , corrected significance level  $p < 0.05$ ). Shaded error bars

represent 1 SEM. Topographic representation (contralateral minus ipsilateral hemisphere) of the contralateral delay activity (C) and alpha lateralization (D) in the time window 300 to 500 msec and 600 to 1100 msec. Average CDA amplitude (E) and alpha lateralization (F) for both dual- and single-task conditions during the two delay intervals, 300 to 500 msec, 600 to 1100 msec. Error bars represent standard errors of the means. (*ns*=non-significant,  $**p < 0.01$ ,  $***p < 0.001$ ).

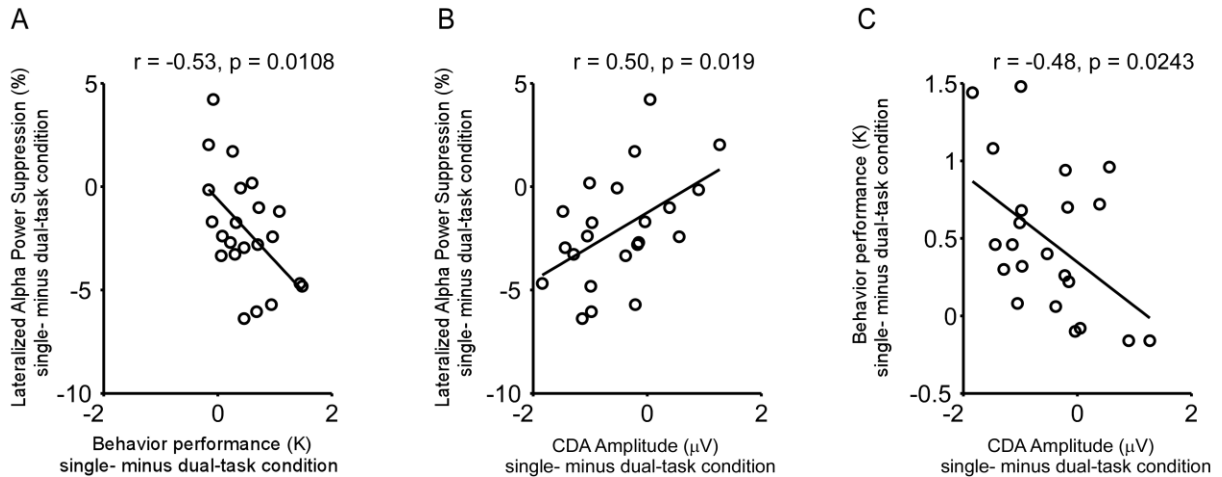


Figure 4. In the late delay interval (600-1100 msec) during which the secondary task was presented, our oscillation measure of visuospatial attention (alpha lateralization) were significantly correlated with the on-line maintenance (CDA) (A) and behavior performance (K) (B). the CDA amplitude in the late interval (600-1100 msec) were also significantly correlated with the behavior performance (K) (C). All measures were computed for the dual-task condition and relative to single-task condition, i.e. the value of each measure in the single-task condition was subtracted from the value of the respective measure in the dual-task condition.

Highlights:

By canceling the time interval between the offset of the secondary task and WM probe, the re-entry of visuospatial attention was prevented before the probe was presented.

Greater reduction of alpha lateralization indicating a more disruption of visuospatial attention was associated with greater reduction of maintenance-related neural activity and larger impairment of behavioral performance.

Even beyond the initial encoding stage, the visual WM system still needs the participation of visuospatial attention to work well

Journal Pre-proof