



Research Report

Working memory biases early object discrimination and parietal activity during attentional selection



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ARTICLE INFO

Article history:

Received 23 August 2021

Reviewed 21 December 2021

Revised 12 May 2022

Accepted 28 August 2022

Action editor Gui Xue

Published online 28 September 2022

Keywords:

EEG

fMRI

N1

Supramarginal gyrus

Inferior parietal lobule

WM-biased attention

ABSTRACT

The contents of working memory (WM) guide visual attention, but the neural mechanisms underlying WM biases remains unclear. Here, we used simultaneous electroencephalography (EEG) and functional magnetic resonance imaging (fMRI) approaches to characterize the timing and location of the neural response underlying WM guidance during a visual search task. Behaviorally, we observed faster search performance when the WM contents matching targets (valid) compared to when WM contents did not reappear (neutral). The EEG data showed similar benefit effects of posterior N1 component, in which targets induced larger N1 amplitudes in the valid condition than in the neutral condition. Interestingly, the fMRI activation in left supramarginal gyrus (SMG)/inferior parietal lobule (IPL) and bilateral occipital cortex was lower in the valid compared to neutral conditions. Importantly, the magnitude of the increased N1 activity and the decreased fMRI activity in the left SMG/IPL predicted the extent of search improvement at an individual subject level. These results suggest that information held in WM enhances early object discrimination during attentional selection, and the left SMG/IPL may be a critical region in mediating goal-directed processing under WM biases in human visual attention.

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<https://doi.org/10.1016/j.cortex.2022.08.009>

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1. Introduction

Working memory (WM) and attention are two critical cognitive abilities in humans, and they interact with each other in a close way (Kiyonaga & Egner, 2013; Soto et al., 2008). Behaviorally, attentional orienting is biased toward the location occupied by stimuli matching the WM contents (Downing, 2000; Han, 2018; Soto et al., 2005). Despite abundant studies that characterize the neural substrates underlying the WM effects on attentional selection processing, the timing and location of these neural mechanisms at play remain a matter of debate.

Electrophysiological methods have been employed to investigate the timing during which the neural response will differ according to the relation between the WM cue and the search target, but findings are inconclusive so far. Some studies showed that the information held in WM could capture attention at the early stage of visual processing, as indexed by the occipito-parietally measured N1 component (Tan et al., 2014, 2015), but others did not find modulations within this early latency (Kumar et al., 2009; Telling et al., 2010). Reasons for the heterogeneities of the scalp-recorded electrophysiological findings might relate to the memory materials and task sets, such as complex irregular pictures that are difficult to verbalize versus colored geometric shapes (Mazza et al., 2011; Tan et al., 2014), and the relative significance of the memory matching stimulus among other stimuli (Tan et al., 2015; Wang et al., 2019). In addition, statistical power might be a critical factor to detect memory-driven attention at early latencies.

Neuroimaging studies provide evidence regarding the neuroanatomic network underlying WM-biased attention processing. Two patterns of neural responses were observed. One is that fronto-temporal–occipital regions showed enhanced activity to the reappearance of WM-matching stimuli in the search array, and the other is that more anterior prefrontal regions and thalamic nuclei were sensitive to the validity of the WM cue (Grecucci et al., 2010; Soto et al., 2007, 2011). Although these studies did not observe strong activation of the parietal cortex associated with WM-based feature guidance on selection, the causal role of the posterior parietal cortex in resolving competition between memory and visual selection has, however, been observed in similar paradigms (Wang et al., 2018). Furthermore, converging neural data from the studies by Soto and colleagues indicate that parietal structure and function predicted individual ability to use the information held in WM to bias perceptual selection (Soto et al., 2014). There is also evidence that the parietal cortex was associated with strategic control over WM biases in human visual attention, for either enhancing or inhibiting biases when WM contents reliably matched targets or distracter stimuli, respectively (Kiyonaga et al., 2014; Soto, Greene, Kiyonaga, et al., 2012). The above findings may be informative about the critical role of the parietal cortex in attentional control over internal WM signals based on selection goals.

The present study utilized a simultaneous electroencephalography-functional magnetic resonance imaging (EEG-fMRI) technique to assess WM biasing during attentional selection

to obtain a further understanding of the neural mechanisms underlying the interplay between working memory and attention. The paradigm was based on previous studies (Kumar et al., 2009; Soto et al., 2007), where subjects hold colors within the same category in WM and to perform concurrently a search task for an unrelated target letter. The match relationship between the target location and the memory content was manipulated, and importantly, the current task used pure visual figures as memory materials because they are difficult to verbalize (Olivers et al., 2006; Wang et al., 2018, 2019). Behaviorally, we expect that WM benefits a search when it matches the sought target, and WM impairs a search when it matches a distractor, as previously found in other studies (e.g., Mazza et al., 2011; Soto et al., 2005). At the electrophysiological level, if the memory color, which is difficult to verbalize, exerts its effect early on subsequent target search, we expected to find larger N1 amplitudes when it contained the target (on valid trials), compared with when it did not reappear in the search display (on neutral trials) and when it contained a distractor (on invalid trials) (Tan et al., 2014, 2015). In terms of the fMRI data, we expected prefrontal activity (e.g., the dorsolateral prefrontal cortex, superior/middle/inferior frontal gyrus) patterns analogous to those reported in Soto et al. (Soto et al., 2007; Soto, Greene, Chaudhary, et al., 2012), showing enhanced activity when the contents of WM matched the critical target of selection. In addition, if the posterior parietal activity (e.g., the supra-marginal gyrus (SMG), superior/inferior parietal lobe (SPL/IPL)) is critical in implementing attentional control over WM biases to optimize goal-directed selection (Kiyonaga et al., 2014; Soto, Greene, Chaudhary, et al., 2012), then the parietal cortex shows decreased activity in the valid trials, since the WM cue benefits target selection thus it is not necessary to recruit the activity of parietal cortex in controlling top-down target selection.

2. Materials and methods

We report how we determined our sample size, all data exclusions (if any), all inclusion/exclusion criteria, whether inclusion/exclusion criteria were established prior to data analysis, all manipulations, and all measures in the study.

2.1. Subjects

Thirty right-handed subjects from the University of Electronic Science and Technology of China (UESTC) were recruited for monetary compensation. All the subjects had normal color vision and had no history of neurological or psychiatric problems. The study was approved by the University of Electronic Science and Technology of China Ethics Board. Written informed consent was obtained from each subject prior to being tested. The methods were carried out in accordance with the approved guidelines, and all experiments conformed to the Declaration of Helsinki. Three subjects were excluded from analyses, resulting in a total of 27 subjects (14 female, mean age 23 years, age range: 19–27). Of these, one subject had a poor task performance (search accuracy below .6), one subject had excessive head movements during fMRI scanning

(exceeding 3 mm in any direction), and one subject had no behavioral data due to the failure of the button box.

2.2. Stimuli and task

Subjects performed the task inside the magnetic resonance imaging (MRI) scanner (GE Signa 3.0 T) with simultaneous EEG and MRI recordings. The sampling clocks of the EEG and MRI systems were synchronized by means of Syncbox (Brain-Products). Fig. 1 illustrates the stimuli and task. The stimuli were displayed using E-Prime 2.0 (Psychology Software Tools, Pittsburgh, PA) and were projected via an liquid crystal display projector onto a flat panel screen placed in front of the MRI scanner with a distance of approximately 55 cm. Subjects viewed the screen through a mirror attached to the head coil. The screen size was 30 cm × 18 cm. The stimuli consisted of 15 colored circles (2.2 cm × 2.2 cm) embedded with the letter ‘T’ or ‘L’ at one of four possible orientations (upright, inverted, rotated 90° clockwise, or rotated 90° counterclockwise). Colors were chosen from five main colors (red, blue, green, purple, or brown). We fixed the hue and value (brightness) of each color and varied the chroma to produce three different colors based on Munsell’s color system. The different color combinations used in this experiment are listed in Table 1. The stimuli appeared against a black background with a central white fixation cross (.8 cm × 1.0 cm). The distance from the center of the stimuli to the fixation cross is approximately 5° of visual angle.

Each trial started with a central fixation for 1 sec, followed by the WM cue circle that was presented for 1 sec. Subjects

Table 1 – The colors used in the experiment.

Munsell (as chosen)			RGB (as measured)		
Hue	Value	Chroma	R	G	B
Green					
5GY	5	2	117	124	102
5GY	5	6	109	129	59
5GY	5	12	98	133	0
Blue					
5PB	5	4	108	122	148
5PB	5	10	74	123	190
5PB	5	16	0	124	235
Purple					
5P	5	6	132	116	142
5P	5	10	149	104	172
5P	5	16	167	88	201
Red					
5RP	5	6	161	106	126
5RP	5	12	196	83	133
5RP	5	16	216	60	138
Brown					
5YR	5	4	151	114	89
5YR	5	8	172	106	52
5YR	5	14	190	97	0

The Munsell values (R = red; P = purple; Y = yellow; B = blue; G = green) were converted to red, green, and blue (RGB) values by a computer program called Munsell Conversion (available from www.gretagmacbeth.com).

were required to remember the color accurately. After a random blank interval of 2 ± 1 sec (1 sec, 2 sec and 3 sec for 1/3 trials respectively), the search arrays were presented for

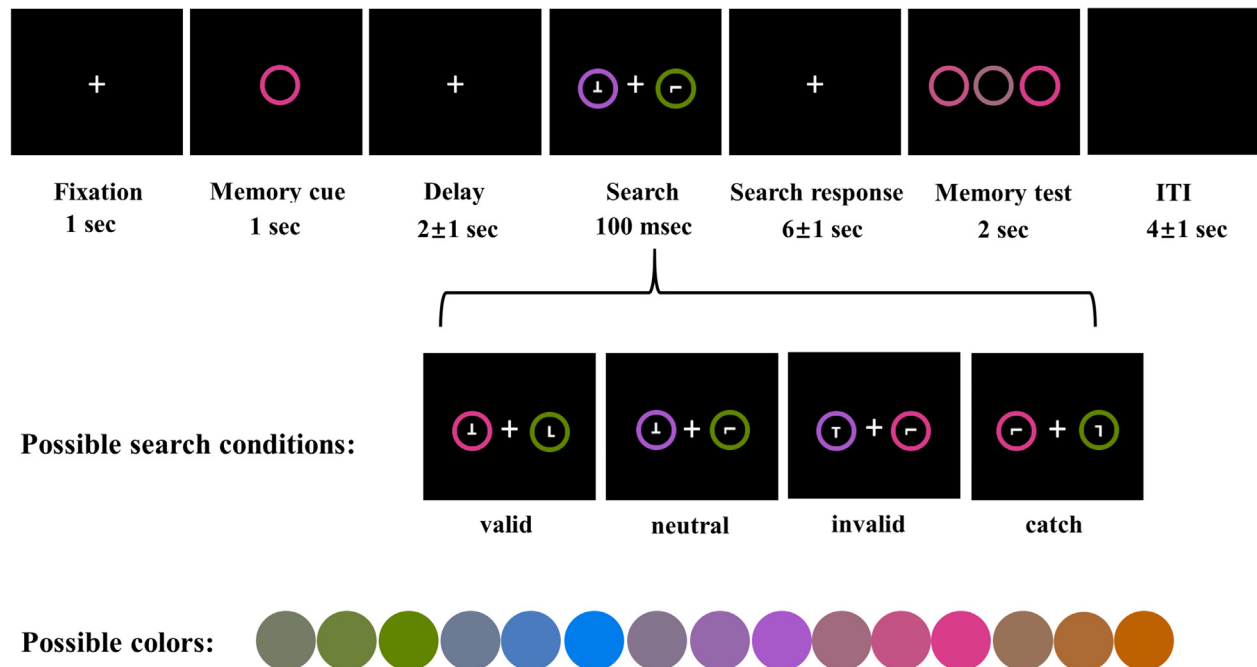


Fig. 1 – Stimulus and trial design. Subjects were asked to memorize the cue for a subsequent memory test. In the retention period, a visual search display was presented for 100 msec, and subjects looked for the target ‘T’ (an upright ‘T’ or an inverted ‘T’) and reported its orientation by manual response. The memorized cue indicated the target location (valid), the distractor location (invalid) or that the target did not reappear (neutral). Additionally, there are catch trials where no target appeared and subjects refrained from responding. In the memory test display, subjects reported the original memorized color within the same color category.

100 msec. Subjects were instructed to maintain their gaze at fixation, to deploy their attention to the target (an upright 'T' or inverted 'T') and to report the orientation of the target by pressing, as quickly as possible, the key '1' or '2' on the numerical keyboard, with the index or middle finger of their right hand, respectively. The target appeared with equal probability at one of the two sides of the screen, 4 cm from the central fixation cross. After a random blank interval of 6 ± 1 sec (5 sec, 6 sec and 7 sec for 1/3 trials respectively), the memory test display was presented for 2 sec. Subjects were required to choose the initial memory cue from three stimuli by pressing the key '1,' '2,' or '3' on the numerical keyboard, with the right index, middle, or ring finger, respectively. After the offset of the memory test display, the intertrial interval (ITI) was randomly varied for 4 ± 1 sec (3 sec, 4 sec and 5 sec for 1/3 trials respectively). During the search, there are three validity conditions regarding the relationship between the WM cue and the search target location. In the first condition (valid condition), the memory cue contained the target letter. In the second condition (invalid condition), the memory cue contained a distracter letter. In the third condition (neutral condition), the memory cue did not reappear in the search display. Additionally, catch trials were introduced to monitor whether subjects were performing orientation-specific discriminations rather than a random key press of either 1 or 2. During the catch trials, no target but only a WM matching distracter was presented, and subjects were asked to withhold response. The selection of the stimuli and their location was equiprobable and randomized. Note that the colors used in the memory test display were chosen from the same color category, thus minimizing the role of verbal encoding. In the search display, the two colors were not selected from the same color category, and they were equally luminant. All the subjects received a memory test practice before the formal experiment. The procedure for the practice test was the same as that described above, except that the search task was removed and feedback was added at the end of each trial, informing subjects whether they made the correct response. This familiarized the subjects with the color stimuli and ensured they could discriminate the colors within the same category. At least two practice blocks were performed before starting the actual experiment to ensure adequate performance (above 60% accuracy for search and memory) and proper maintenance of eye fixation. The horizontal electrooculogram (HEOG) was calculated as the difference in activity between F7 electrode and F8 electrode, which was used to measure horizontal eye movements. Two subjects were excluded from analyses due to excessive horizontal eye movements. The maximal amplitude of the HEOG was 8 μ V for any remaining subject, which indicated that the average eye-movement was less than .5° toward the target (Lins et al., 1993; Yang et al., 2017).

Each subject completed 8 blocks of 16 trials, where each block included 4 valid, 4 neutral, 4 invalid and 4 catch trials. The trials were randomly intermixed within a block, and subjects were not aware of these conditions before the experiment. The data for two blocks for three subjects of the remaining 27 subjects were missing due to machine recording problems. Each block lasted 268 sec, and the fMRI scan lasted approximately 1.5 h, including the task scan, the T1-weighted structure MRI scan, and the breaks between the scans.

2.3. Behavioral data analysis

The mean accuracy (ACC) for the search task and mean reaction times (RTs) for the correct search trials were evaluated using the correct WM trials across the subjects. A repeated measure analysis of variance (ANOVA) was performed with condition as within-subject factors. Post hoc paired t-tests with Bonferroni correction for multiple comparisons were applied when necessary. Mean values $\pm$ standard errors of the mean (SEM) were reported for the behavioral results. All statistical analyses were performed using SPSS Statistics Release 19 (IBM, Somers, NY, USA).

2.4. EEG recording and preprocessing

Electroencephalography (EEG) signals were collected using a 64-channel Neuroscan Maglink System, which is compatible with MRI. Vertical electrooculograms (VEOGs) and electrocardiograms (EKGs) were recorded with additional electrodes placed above and below the left eye and the left sternum, respectively. The sampling rate was 1000 Hz, and the electrode impedances were kept under 10 k Ω throughout the experiment. The AFz electrode site served as a ground electrode, and an electrode between Cz and Pz served as a reference.

EEG data preprocessing was performed using the CURRY 7 Neuroimaging Suite (Neuroscan, Charlotte, NC). MRI gradient artifacts were removed using averaged artifact subtraction (AAS) during each repetition time (TR) interval (Allen et al., 2000). Ballistocardiographic (BCG) artifacts were identified using the electrocardiogram (EKG) channel with a template matching procedure, and removed using the principal component analysis (PCA) with top 3 components for correction. Subsequent all EEG analyses were carried out using the EEGLAB toolbox (Delorme and Makeig 2004) and custom scripts implemented in MATLAB (The MathWorks, Inc., Natick, MA). Data were re-referenced against the average of all channels, and filtered with a bandpass filter of .1–48 Hz. Independent component analysis (ICA) was then performed on the scalp EEG for each subject to identify and remove components that were associated with blinks and eye movements (Bae and Luck 2018). The continuous ICA-corrected EEG data were segmented from –200 to 800 msec relative to the onset of search displays. The event-related potentials (ERPs) were baseline corrected to the 200 msec pre-onset of search display and separated according to experimental conditions.

2.5. ERP analysis

Event-related potential (ERP) waveforms were extracted by averaging trials according to validity conditions (valid, neutral, invalid). Based on the grand-average ERP waveforms and the topographical maps, the N1 analyses were focused at lateralized electrodes PO3, PO5, PO7, PO4, PO6, PO8. The N1 component was quantified as the mean amplitude in the post-stimulus interval 170–200 msec. These values were submitted to a 1×3 repeated-measures ANOVA with the validity (valid, neutral, invalid) as factors. Post hoc paired t-tests with Bonferroni correction for multiple comparisons were applied when necessary.

Since the N2 posterior contralateral (N2pc) is a well-known indicator of attention allocation in visual search (Eimer and Grubert 2014; Li et al., 2013; Liu et al., 2016), we did consider whether the N2pc is affected by top-down effects of a prime held in WM. Therefore, we tried to extract the contralateral and ipsilateral attentional responses to lateral target at posterior and lateral occipital electrodes. The results of this analysis do not indicate any clear N2pc evidence for the interplay between WM and visual search. Further details on the results of lateralized components across different validity conditions can be found in the Supplementary Materials.

2.6. fMRI data acquisition and preprocessing

Magnetic resonance imaging (MRI) scanning was performed using a 3.0 T GE Sigma scanner at the University of Electronic Science and Technology of China, Chengdu, China. Functional data were acquired using a gradient echo planar imaging (EPI) sequence with the following scanning parameters: 134 EPI volumes; repetition time (TR) = 2000 msec; echo time (TE) = 30 msec; flip angle (FA) = 90°; field of view (FOV) = 240 mm; matrix size = 64 × 64; voxel size = 3.75 × 3.75 × 3 mm³; 43 slices. Structural data were acquired using a high-resolution T1-weighted scan (voxel size = 1 × 1 × 1 mm³, 176 slices). All images were acquired parallel to the anterior–posterior commissural line.

All analyses were performed using SPM12 (statistical parametric mapping software, <http://www.fil.ion.ucl.ac.uk/spm>). The first five EPI volumes of the fMRI images were discarded for signal stabilization. fMRI data preprocessing included slice timing correction, three-dimensional motion correction, coregistration to individual anatomical images, normalization to the Montreal Neurological Institute (MNI) reference space (3 × 3 × 3 mm³), and spatial smoothing with an 8 mm Gaussian kernel (full-width at half maximum).

2.7. fMRI data analysis

For the first-level statistical analyses, a general linear model (GLM) was constructed for each subject via regressors corresponding to the onset of the memory cue (duration set to 7 sec) for each condition, resulting in 4 regressors of interest. In addition, a separate regressor was used to model the onset of the memory test displays. All the regressors were convolved with the canonical hemodynamic response function (HRF) provided in SPM12. Six additional spatial movement regressors were added to the design matrix.

Single-subject contrasts were then calculated to establish the hemodynamic correlates of each search condition with the fixation baseline. Group effects were subsequently assessed by submitting the individual SPMs to paired t-tests where participants were treated as random effects. Significance for whole-brain analyses was set at a threshold of $p < .05$ family-wise error (FWE) corrected for multiple comparisons at the cluster level with an underlying voxel level of $p < .005$ uncorrected (Woo et al., 2014).

Regions of interest (ROIs) were defined based on the group effects. Specifically, a 9-mm radius sphere centered around the peak activation of each cluster was drawn as an region of interest (ROI) by means of MarsBar software (<http://marsbar>.

sourceforge.net). The beta coefficients of each ROI were then calculated for each of the search conditions, and subsequently used as seed in the psychophysiological interaction (PPI). The mean signal intensity of the ROI during the fixation epochs was used as baseline. These values were entered into a repeated measure analysis of variance (ANOVA), with condition as within-subject factors. Linear regression models were used to evaluate the relationship between behavioral performance and fMRI activity.

PPI analyses: To assess whether the observed core regions that showed a validity effect are functionally coupled with other regions, we conducted a generalized psychophysiological interactions (PPIs) analysis (gPPI; <https://www.nitrc.org/projects/gppi> (McLaren et al., 2012)). Briefly, the BOLD time series of activity from seed regions were extracted for each run as the volumes of interest (VOIs). Then, the PPI parameters of each experimental condition (valid, neutral, invalid) were calculated. Lastly, these PPI parameters were entered into GLMs as the regressors to find the regions which showed significant correlations with the interaction between the physiological signal (e.g., from the left supramarginal gyrus (SMG)) and the psychological context of the validity conditions. The group PPI effects for each seed region were tested using paired t-tests between different conditions. Significance for whole-brain analyses was set at a threshold of $p < .05$ FWE corrected for multiple comparisons at cluster level with an underlying voxel-wise primary $p < .005$ uncorrected.

EEG-informed fMRI Analysis: In order to investigate cortical activity that showed unique covariation with early visual processing during attention selection, the normalized (z-scored) single-trial N1 values for each experiment condition were included as parametric regressors in the fMRI data analysis (4 additional regressors). GLM analysis of fMRI data was identical to that described above, except for the addition of these parametric regressors. We then identified brain regions showing significant covariation of N1 amplitudes with BOLD response for each validity condition. Significance for whole-brain analyses was set at an uncorrected threshold of $p < .005$ at voxel level, which has been used in several simultaneous EEG-fMRI recording studies (Liu, Bengson, Huang, Mangun, & Ding, 2016; Warbrick et al., 2014), and the activated cluster contains at least 5 voxels were adopted.

3. Results

3.1. Working memory bias attentional selection in behavior

Subjects correctly reported the location of the memory cue with a mean accuracy of 83.68% (standard deviation = 8.66%). A 1 × 3 repeated ANOVA comparing the search performance with the three validity conditions as factors revealed a significant main effect for the search RTs [$F(2,25) = 4.319$, $p = .024$, and $\eta^2_p = .257$], but no significant main effect was observed for the search ACC ($p > .1$). Post hoc paired t-tests, using Bonferroni correction for the three possible comparisons across the three validity conditions, revealed significantly decreased search RTs for the valid (973.067 msec) condition compared to the neutral (1020.322 msec) condition ($t(26) = 2.892$, $p = .023$).

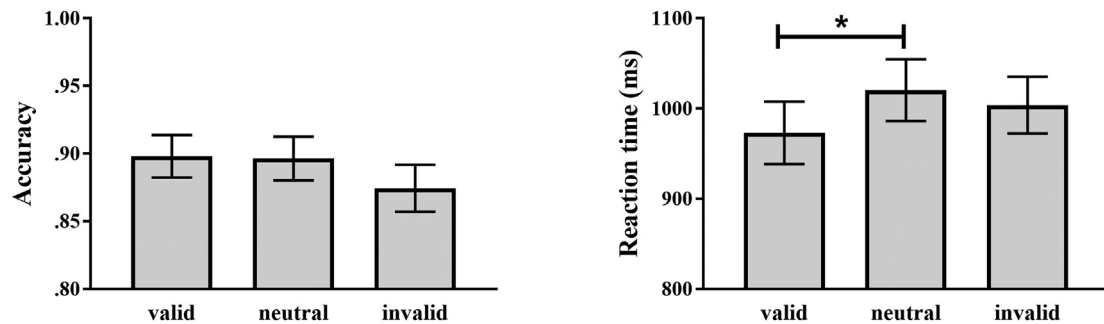


Fig. 2 – Working memory bias attentional selection in behavior. Mean search accuracies and reaction times (RTs) of the correct search trials are shown for the 27 subjects in the correct WM trials across different validity conditions. Error bars show the standard error of the mean (SEM), and asterisks mark significant post hoc paired t-test using Bonferroni correction for multiple comparisons ($*p < .05$).

(see Fig. 2). No significant differences were observed between other two conditions (all $p > .1$).

3.2. Working memory bias early object discrimination in the N1 time window

Fig. 3a depicts the grand-average ERPs recorded at the posterior ROI (PO3/PO5/PO7/PO4/PO6/PO8) for the three validity conditions. There is a large negative deflection occurring within the time window of 170–200 msec, that is, the N1 component. A 1×3 repeated-measures ANOVA on the N1 amplitudes was performed with validity as factors. We found a significant main effect for validity [$F(2,25) = 4.339$, $p = .024$, and $\eta_p^2 = .258$], showing larger N1 amplitudes in the valid conditions ($-5.412 \mu V$) compared to the neutral conditions ($-3.434 \mu V$) [$t(26) = 2.846$, $p = .026$, Bonferroni

corrected for multiple comparisons; Fig. 3b]. No significant differences were observed between other two conditions (all $p > .1$).

3.3. Brain activity under working memory biases in visual attention

A whole-brain contrast analysis showed significantly decreased activations of valid condition relative to neutral condition in the left parietal cortex (supramarginal gyrus/inferior parietal lobule/postcentral gyrus), and bilateral occipital cortex (lingual gyrus/calcarine) (cluster-level $p < .05$ FWE corrected) (see Table 2/Fig. 4a). In the contrast of valid vs invalid and invalid vs neutral, no suprathreshold cluster was found. Two regions of interest (ROIs) were selected as the site of maximal activation in the activation clusters, based on

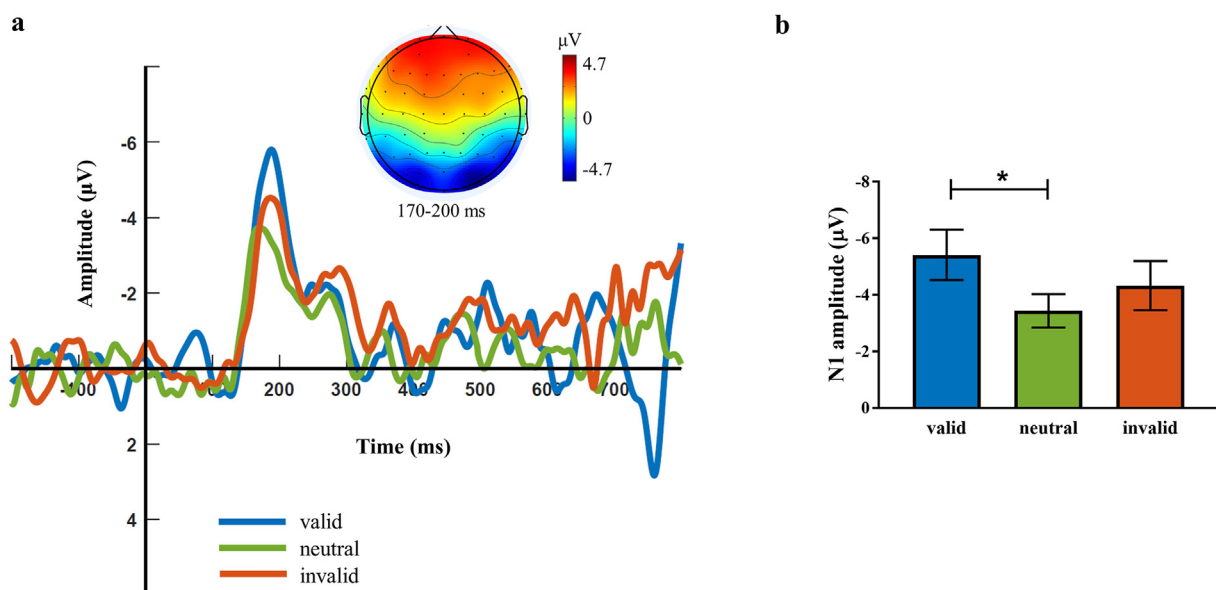


Fig. 3 – Working memory bias early object discrimination in the N1 time window. (a) Grand-average ERP waveforms are time locked to the onset of the search display on six posterior electrodes (PO3/PO5/PO7/PO4/PO6/PO8). Search targets elicited an N1 (170–200 msec) component, and gray shaded rectangles show the N1 time window for statistical analyses. (b) The mean N1 amplitudes for the three validity conditions are shown on the right side. Error bars show the standard error of the mean (SEM), and asterisks mark significant post hoc paired t-test using Bonferroni correction for multiple comparisons ($*p < .05$).

Table 2 – Cue-validity effects: valid < neutral.

Cluster	Anatomical regions	Hemisphere	T	Cluster peak (x, y, z)			No. of voxels
1	Supramarginal gyrus/inferior parietal lobe/postcentral gyrus	L	–3.98	–45	–27	39	329
2	Lingual gyrus/calcarine	L/R	–4.25	–6	–69	–3	445

Coordinates (x, y, z) correspond to the MNI (Montreal Neurological Institute) space.

the contrast valid-neutral in whole brain analysis, which are the left supramarginal gyrus/inferior parietal lobule (MNI: –45, –27, 39) and the lingual gyrus (MNI: –6, –69, –3). Since the search RTs were significantly faster in the valid condition

than that in the neutral condition and the brain activity was significantly weaker in the valid condition than that in the neutral condition, we tried to find the correlation between the two. The results show that the search RT decrease from the

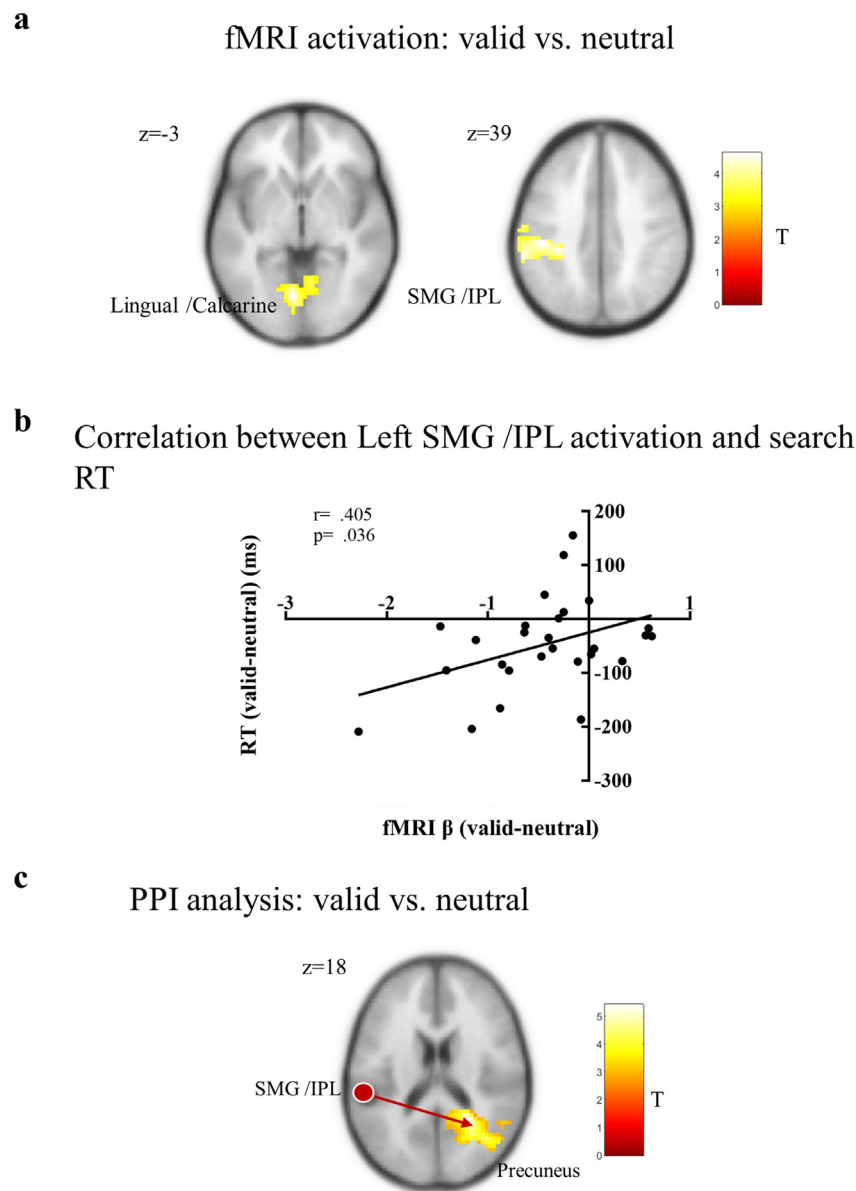


Fig. 4 – fMRI results. (a) Displayed are regions which showed increased activation in the neutral condition as compared to the valid condition. $p < .05$, FWE corrected at cluster-level. **(b)** The extracted beta coefficients from left SMG/IPL showed significant correlation (Pearson's r) with the search reaction times in the difference between valid and neutral conditions. The correlation remained significant after Bonferroni correction for multiple testing. **(c)** The functional coupling between left SMG/IPL and right precuneus was found to be increased in the neutral condition compared with the valid condition. $p < .05$, FWE corrected at cluster-level.

neutral condition to the valid condition was positively correlated with the brain activity decrease from the neutral condition to the valid condition in the left SMG/IPL ($r = .405$, $p = .036$), which remained significant after Bonferroni correction for multiple testing (see Fig. 4b). We found no correlation between the brain activity and search reaction times in the lingual gyrus ($p > .1$).

According to the above whole-brain contrast analysis results, two ROIs (left SMG/IPL and lingual gyrus) were taken as seed regions with a 9 mm radius sphere centered at the peak activation coordinates. The total PPI effects showed significant interactions of the left SMG/IPL with the right precuneus in the contrast of valid < neutral (cluster-wise $p < .05$ FWE corrected with primary $p < .005$, see Table 3/Fig. 4c). There was no significant functional connectivity detected for the seed region of the lingual gyrus in the contrast of valid vs neutral. And no significant PPI effects were observed in the contrast of valid vs invalid and invalid vs neutral using either the left SMG/IPL or lingual gyrus as seed.

The EEG-informed fMRI analyses including N1 component as parametric regressors yielded significant results only for the valid condition. Fig. 5 depicts the brain regions that showed covariation with N1 amplitudes in the valid condition, including the right insula, the right thalamus and the bilateral putamen (see also Table 4, voxel-wise $p < .005$ uncorrected). No significant covariations were found for neutral and invalid trials.

4. Discussion

The behavioral results suggest that the memorized color benefits searching when its contents overlap with the sought target, as indicated by faster search RTs during the valid condition compared to the neutral condition. This is consistent with several findings in the literature regarding memory-based attentional capture (Kim & Cho, 2016; Soto et al., 2006). However, no RT costs were observed when the target and the WM item were at different locations, that is, the search RTs were not slowed in the invalid condition compared to the neutral or valid conditions. This finding was inconsistent with the proposal that working memory could involuntarily capture attention (Soto et al., 2008). In a comparable fMRI study, researchers found significant RT cost but no RT benefit of the WM cue on visual search, despite they used similar two-object search tasks (Soto, Greene, Chaudhary, et al., 2012). The discrepancy could be due to the fact that the overall RTs of the search task reached ceiling in this study, with an average RTs less than 600 msec (valid: 518.3 msec; neutral: 526.24 msec;

Table 3 – PPI effects with left SMG/IPL as seed: valid < neutral.

Anatomical regions	L/R	T	Cluster peak (x, y, z)	No. of voxels
Precuneus	R	–5.40	24 –51 18	378
Coordinates (x, y, z) correspond to the MNI (Montreal Neurological Institute) space.				

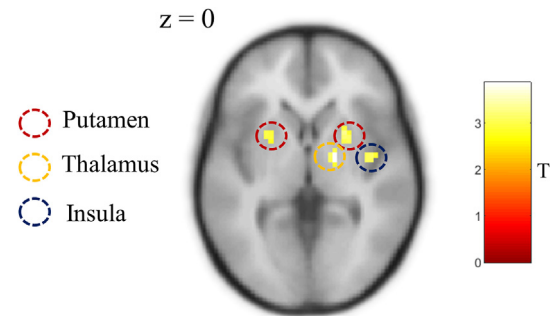


Fig. 5 – N1-informed analysis for the valid condition. Activations are whole-brain corrected at $p < .005$ uncorrected at voxel level.

invalid: 571.58 msec). It is possible that working memory cannot further facilitate search performance, resulting in no RT benefit observed. While in the present study, the overall search RTs is over 900 msec (valid: 940.12 msec; neutral: 987.45 msec; invalid: 971.98 msec), the WM cue benefit effects may override the cost effects in such a stressed visual search task.

The ERP results showed that the search target elicits a larger posterior lateralized N1 amplitude in valid trials than in neutral trials. The N1 component is a robust electrophysiological marker for early attentional modulation (Wang et al., 2012). It has been shown that the N1 amplitude is larger for attended location stimuli than for unattended location stimuli and that the N1 wave reflects a discrimination process that is applied to the attended location (Hong et al., 2017; Wang et al., 2012). In the current study, the WM representation produced a top-down attentional allocation toward the memory-matching location, as reflected in the N1 amplitude. When the memory content and the search target spatially overlap, the attentional processing of the target is enhanced and induces a larger N1. Similar to the behavioral results, no significant N1 amplitude difference was found between the invalid condition and the neutral condition, which may reflect the attentional offset effect between memory stimuli and search target stimuli in opposite positions. These results imply that the ERP measure is consistent with the behavioral performance, both showing a further enhanced target selection processing in the valid compared to the neutral conditions at an early stage.

Interestingly, our evidence that WM affects attention processing at an early stage seems to be in disagreement with

Table 4 – Summary of N1 covariations: valid.

Anatomical regions	L/R	T	Cluster peak (x, y, z)	No. of voxels
Thalamus	R	3.86	18 –9 0	7
Insula	R	3.02	42 –9 0	12
Putamen	L	2.91	–24 6 0	7
Putamen	R	3.27	24 9 0	9
Coordinates (x, y, z) correspond to the MNI (Montreal Neurological Institute) space.				

some other studies in which WM guidance was only found on the later N2-posterior contralateral component (N2pc) (Kumar et al., 2009; Mazza et al., 2011; Telling et al., 2010), P3 (Kumar et al., 2009), and sustained posterior contralateral negativity (SPCN) components (Wang et al., 2019). These variable findings concerning ERP correlates of memory-guided attentional processing could reflect task differences that affect the locus of attentional selection. Previous researchers have used a briefly flashed search display (94–164 msec) to found that WM could boost early perceptual processing at the location occupied by the matching item rather than the contents of WM biasing selection at a “late” level in favor of matching objects (Soto, Wrigglesworth, Bahrami-Balani, & Humphreys, 2010). In our procedure, the search exposure was as brief as 100 msec, which is similar to the time used in the above study. Thus, it is more likely to detect the N1 difference between conditions by the current task setting than by studies that used longer search durations. On the other hand, according to the perceptual load theory of selective attention, the perceptual capacity is consumed by target-related information, and distractor processing is reduced during high perceptual load conditions, producing early target selection effects, while late selection typically occurs in situations of low perceptual load (Lavie et al., 2004). In the present study, the physical characteristics of the matching distractor differ from those of the other distractor only in color during the search, and the overall search RT is over 900 msec. For those finding later selection effects, the WM matching distractor differs from others in color and shape, and the overall search RT is around 600–700 msec (Kumar et al., 2009; Mazza et al., 2011). It is possible that the perceptual load during the search is higher in the present study than that in previous studies; thus, the modulation of attentional selection by working memory occurs during the N1 time window.

Compared with the condition that the WM cue did not appear in the search display (neutral), the fMRI activities in the left supramarginal gyrus (SMG)/inferior parietal lobe (IPL) were reduced when the WM cue reappeared in the search display and were consistent with the target location (valid). Previous studies have indicated the critical role of the parietal cortex in the control of top-down modulation of the visual cortex (Bressler et al., 2008; Ruff et al., 2009; Silvanto et al., 2009). For example, an fMRI study on visual search showed that the activity of the superior/inferior parietal lobe increased during the hard within category search (find target letters among distracting letters) compared to the easy between category search (find target letters among distracting numbers). Furthermore, the faster the subjects responded in the visual search, the stronger the functional connectivity between the superior parietal lobe (SPL) and the primary visual cortex (V1) (Bueichekú et al., 2015). In the valid condition, the search processing was promoted by the WM color, and it was not necessary to recruit the activity of the parietal cortex in controlling top-down target selection, resulting in reduced BOLD activity in the valid condition compared to the more difficult neutral condition. Other studies have described the role of the posterior parietal cortex in suppressing the attentional capture of salient stimuli (Mevorach et al., 2010) or irrelevant working memory content (Soto et al., 2011, 2014). In

particular, the supramarginal gyrus has been shown to be involved in mediating competition between visual inputs (Chambers et al., 2006). In the valid condition, the memory content cooperated with the search processing, which promoted the target search. Subjects did not need to inhibit the content of working memory, thus showing a small fMRI activity in the SMG/IPL. In addition, correlation analysis showed that the activity difference of the left SMG/IPL under valid and neutral conditions was positively correlated with the difference in RT under valid and neutral conditions; that is, the greater the WM benefit on search performance, the greater the brain activity difference in the left SMG/IPL between the valid and neutral conditions. This indicates that the activity of the left SMG/IPL is consistent with the search behavior. When the memory content promotes the search, the participation degree of the left SMG/IPL decreases.

To delineate the neural circuitry supporting target selection during the interplay between internal WM content and external visual attention, the interregional interactions were considered through PPI analyses. The results showed decreased functional connectivity between the left SMG/IPL and the right precuneus during the valid condition compared with the neutral condition. This finding implies that target selection may depend upon functional coupling between the left SMG/IPL and the right precuneus that has been proven to be associated with filtering of task irrelevant features (Reeder et al., 2017) and maintaining attention on goal-related stimuli (Ferri et al., 2016). In the other word, the decreased functional connectivity might signal decreased attentional effort to the target under valid conditions due to the WM cue benefit effects.

In accordance with our findings, the validity effects of the WM contents on selection in the intraparietal sulcus have been previously reported (Soto, Rotshtein, et al., 2012). Further findings indicate that both the structure and function of the left parietal cortex mediate the expression of WM biases in human visual attention (Soto et al., 2014). Our results extend these findings to specify that left SMG/IPL functioned importantly during the goal-directed attentional selection during the interplay between working memory and visual search. It's worth noting that prefrontal regions have previously been found to be involved in the WM-guided visual search (Grecucci et al., 2010; Soto et al., 2007; Soto, Rotshtein, et al., 2012). These inconsistent findings could be due to the difficulty of memory in this study (memory task ACC = .818) is greater than that in the studies mentioned above (e.g., memory task ACC is .967 for Grecucci et al., 2010, .95 for Soto, Rotshtein, et al., 2012, .890 for Soto et al., 2007). Studies have found that the WM guiding effects are less likely to invoke frontal regions associated with cognitive control under high memory load (Soto, Greene, Chaudhary, et al., 2012).

In order to investigate cortical activity that showed unique covariation with early object discrimination during attentional selection, EEG-informed fMRI analysis was performed. When the WM contents overlap with the sought target (valid condition), the N1 amplitudes showed significant covariations with right-lateralized activations of the insula and the thalamus, and the bilateral putamen. Neurons in the putamen have recently been evidenced to be involved in the object

discrimination by their visual features (Kunimatsu, Maeda, & Hikosaka, 2019) and the right rolandic operculum that covers the insula has been suggested to be at the heart of the ventral attention system (Eckert et al., 2010). In addition, the thalamus nuclei has been found to be critical in controlling visual attention (Jagtap & Diwadkar, 2016), particularly in guiding attention based on goal-relevant information held in pre-frontal areas linked to WM (De Bourbon-Teles et al., 2014; Soto et al., 2007; Soto, Rotshtein, et al., 2012). The covariations of these brain regions with trial wise N1 amplitudes reveal that variations in early activity in the occipitotemporal cortex have a measurable influence on higher-order cognitive functions of target discrimination and attentional selection. Importantly, despite identical visual input, these covariations were limited to valid condition, showing their sensitivity to the attentional biases from the contents of working memory. Note however that these findings were generally statistical weaker, as no region showed a covariation strength that reached the significance of $p < .05$ FWE corrected for multiple comparisons at the cluster level, we therefore take these findings with a grain of salt.

5. Limitations and future directions

Although N1 has been reported to be involved in early object discrimination from a variety of studies incorporating attentional tasks (Bocca et al., 2015; Li et al., 2010), observation of attention-related N2pc components will provide a more comprehensive understanding of WM's effect on attentional selection. However, in the current study, we did not find any clear evidence for the N2pc component. It is possible that, as noted earlier, the high perceptual load in this study may be responsible for the early attentional processing differences. On the other hand, the present study might have included too few trials per condition for such an effect to surface. We note that previous relevant studies set up at least 125 trials per condition to observe reliable N2pc (Kumar et al., 2009; Mazza et al., 2011; Wang et al., 2019) while one condition in the current study has 32 trials. Balancing sufficient number of trials to detect potential ERP components and acceptable duration of MRI scans is a matter of consideration for future simultaneous EEG-fMRI studies.

6. Conclusion

We observed that the representation held in WM biased object discrimination at the early attentional processing stage, as reflected in the N1 time window. And the facilitated target selection results in decreased activation of parietal control regions including the left supramarginal gyrus/inferior parietal lobe, regions of the occipital cortex including the lingual gyrus/calcarine. Furthermore, the functional coupling between the left SMG/IPL and the right precuneus is decreased during valid trials, compared to neutral trials. The current findings extend previous work to show the left SMG/IPL may be a critical region in mediating goal-related processing under WM biases in human visual attention.

Credit authorship contribution statement

Min Wang: Conceptualization, Investigation, Methodology, Writing – original draft, Writing – review & editing. **Ping Yang:** Methodology, Software, Visualization. **Tingting Zhang:** Data collection. **Wenjuan Li:** Data collection. **Junjun Zhang:** Conceptualization, Funding acquisition. **Zhenlan Jin:** Conceptualization, Funding acquisition. **Ling Li:** Conceptualization, Data curation, Formal analysis, Funding acquisition, Resources, Supervision, Validation.

Open practices

The study in this article earned Open Data and Open Materials badges for transparent practices. Materials and data for the study are available at <https://osf.io/369b5/>.

Declaration of competing interest

None. No part of the study procedures or study analyses was pre-registered prior to the research being conducted.

Data availability

Data will be made available on request.

Acknowledgments

This work was supported by grants from the NSFC [grant numbers 62176045, 32060198, 32100847, 32260211], the Programme of Introducing Talents of Discipline to Universities (the 111 project) [grant number B12027], the Fundamental Research Funds for the Central Universities [ZYGX2020FRJH014], MOE (Ministry of Education in China) Liberal Arts and Social Sciences Foundation (21YJC190019), Guizhou Education Department Youth Science and Technology Talents Growth Project (KY [2021]143, KY[2022]213), Guizhou Science and Technology Department (ZK[2021]116).

Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.cortex.2022.08.009>.

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