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RESEARCH ARTICLE

The success of the representation maintenance affects the memory-guided search processing: an ERP study

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Abstract

Previous evidence showed that working memory (WM) contents can bias visual selection. However, less is known about how the WM effects change when the WM representation is not held successfully. Here, we investigated this problem using event-related potentials. Subjects maintained a color in WM while performing a search task. The color cue contained the target (valid) or the distractor (invalid). Subjects could either remember the color accurately (correct WM) or not (incorrect WM). An N2-posterior contralateral component and a sustained posterior contralateral negativity (SPCN) were recorded in the valid and incorrect WM condition, while only an attenuated SPCN was elicited in the valid and correct WM condition. No reliable lateralized components were found for the invalid trials. These findings suggest that the WM effects on visual search are affected by the resource interchange between WM and search processes.

Keywords Visual search · Working memory · N2pc · SPCN · Competition · Processing resources

Introduction

Working memory (WM) refers to the online maintenance and manipulation of information that is no longer present in the environment (Baddeley 2003). Selective attention reduces the load on limited-capacity cognitive systems by filtering irrelevant information from the stimulus stream (Gorgoraptis et al. 2011). Behavioral studies indicate that the contents of WM bias attention toward the object whose features were pre-activated from WM (Soto et al. 2005; Hollingworth et al. 2013b).

Event-related potential (ERP) studies reveal that WM has an involuntary effect on early attention selection for the search target, as reflected by the N2-posterior contralateral component (N2pc), typically occurring 200–300 ms post-stimulus onset, which was used to index attentional selection process (Telling et al. 2010; Mazza et al. 2011). Evidence showed enhanced N2pc amplitudes for the search target when it appeared on the same side as the WM prime, compared with when the prime did not reappear on the search display, and when the prime was contralateral to the target (Kumar et al. 2009). A following ERP component, named sustained posterior contralateral negativity (SPCN), is thought to reflect the post-selection processing, where the search target is further analyzed and identified in working memory (Hilimire et al. 2011). It has a similar scalp distribution to N2pc, but has a later onset (about 350 ms post-stimulus onset) (Mazza et al. 2007). Evidence showed that a target-elicited N2pc and a SPCN were attenuated in the presence of a distractor when the target features were unknown compared to a condition where the target features are known in advance (Eimer et al. 2011). Thus, the findings suggest that top-down information (another form of WM) is able to accelerate target selection by preventing distracting information from attracting attention and entering into working memory.

Few studies have used ERP measures to explore the differential effects of working memory on early attention selection vs. late representation processing, and how these are influenced by the competitive interaction between WM representation and search target representation. We used a

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paradigm based on Soto et al.'s (2006) study (Soto et al. 2006), where subjects maintained a color in WM while performing a search task. We wanted to investigate whether successfully holding a color in WM would alter target selection and target identification during the visual search. To this end, we included the incorrect WM trials and focused on the N2pc and the SPCN components to directly measure the early selective attention and the subsequent processing of search targets in working memory during a visual search. We hypothesized that search performance was facilitated in the valid relative to the invalid WM conditions, as reflected by enhanced N2pc and SPCN in the valid condition but not in the invalid condition. Furthermore, we expected to see a competitive interaction between WM representation and search target representation, especially when they are spatial overlap, since a common pool of resources seems to support both of these processes (Woodman and Luck 2004; Emrich et al. 2009). If the subjects maintain their focus on maintaining the WM representation, this may lead to less resource for search target attention and identification. In contrast, better performance in target identification may make it difficult for subjects to maintain the precise color of WM item. We hypothesized a relatively large N2pc and SPCN for the search target in the incorrected WM trials, and a relatively small N2pc and SPCN in the corrected WM trials.

Materials and methods

Participants

Fourteen right-handed students from the University of Electronic Science and Technology of China (UESTC) were recruited for monetary compensation. All the subjects (6 females, mean age 23.6, range 21–26) 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 signed by each participant in accordance with an experimental protocol that conformed to the Declaration of Helsinki.

Stimuli and task

All the stimuli (1.8° × 1.8°) appeared against a black background with a central white fixation cross subtending 0.38°. Colors were chosen from the 1976 CIE *L a* b** color space. We fixed the luminance at $L = 64$ and varied the a^* and b^* parameters to produce 12 different colored squares. The colors can be divided into six categories. Within the category, the color value was selected randomly from two similar colors. We manipulated the variants of the same color to confirm the difficulty of memorizing the color and to ensure that there are enough memory error trials for analysis.

An example of the experiment can be seen in Fig. 1a. Task trials began with a 400 ms central fixation, followed by the WM cue that was presented for 300 ms. Subjects were required to remember the color accurately. After a delay of 700 ms, the search arrays were presented for 600 ms. Each contained six colored squares evenly distributed around a central fixation cross at a radial distance of 3.2°. One of the colors was the same as the WM cue, while the others were randomly selected without replacement from the remaining five color categories (two colors were not selected from the same color category). Each square contained a letter 'T' or 'L' at one of four possible orientations (90°, 180°, 270°, 360°). Subjects were required to look for the target (an upright 'T' or inverted 'T', one of which was presented on each trial) and report its orientation by pressing the keys '1' and '2' on a computer keyboard with the index or middle fingers of their right hand as quickly as possible. The target appeared with equal probability at one of the four lateral positions, but never at the top or bottom position. The memory color contained the target letter (valid trial) or the distractor letter (invalid trial). In the invalid condition, the memory color appeared at one of the two lateral positions at the opposite side of the target letter. The fixation cross remained until a response was given or after a designated time had elapsed (2000 ms). Subsequently, the memory test displays (the colors were from the same category) were presented until a button response was obtained or after a designated time had elapsed (2000 ms). Subjects were required to choose the WM cue by pressing the keys '1' and '2' on a computer keyboard with the index or middle finger of their right hand. This within-category discrimination task minimized the role of verbal encoding. The memory test results served as a measure of whether the color was maintained successfully (correct WM) or not (incorrect WM). Combining the two types of memory test results with the two types of search conditions, we obtained four types of conditions for the search display: valid and correct WM, valid and incorrect WM, invalid and correct WM and invalid and incorrect WM. After the memory test display offset, a final "end" screen was displayed (1000 ms; 'The end!'). Successive trials began immediately after this final display. Stimulus–response mappings remained constant for each subject throughout the experiment and were counterbalanced across subjects.

Each subject completed two practice blocks of 50 trials, and 12 test blocks. Each block included 25 valid trials and 25 invalid trials. The trials were randomly intermixed within a block and subjects were not aware of the valid and the invalid conditions before the experiment. Central fixation was required during the experiment.

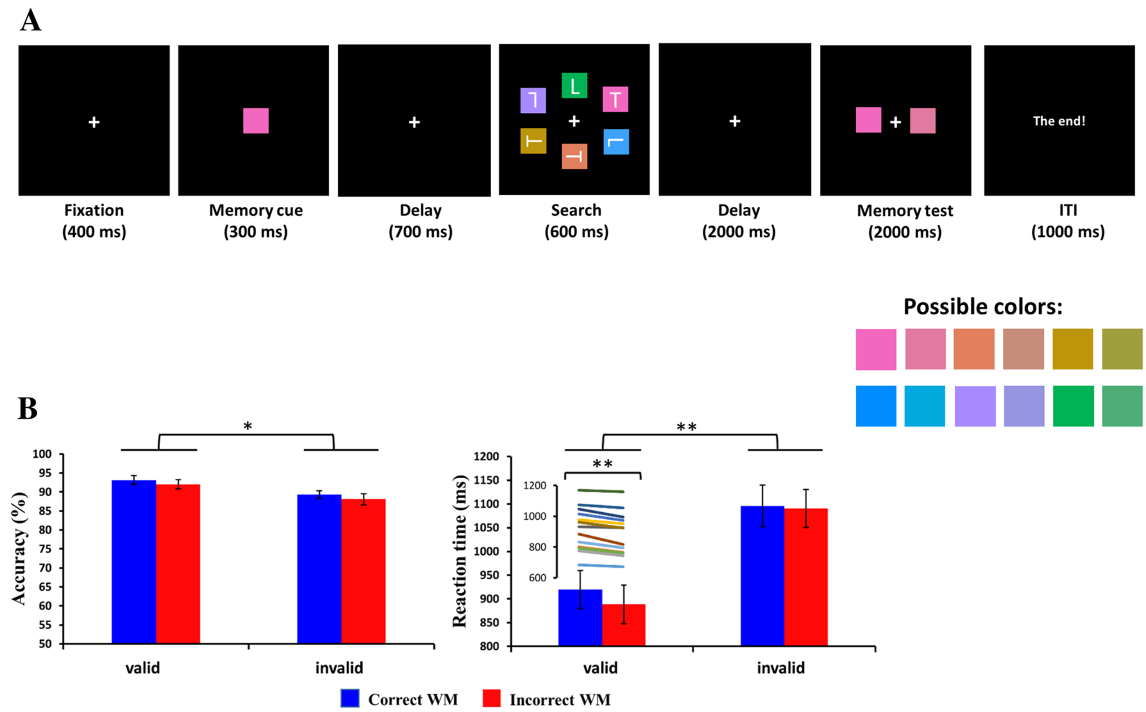

Fig. 1 Experimental paradigm and search performance. **a** Each trial began with a 400 ms fixation; then the memory cue was presented for 300 ms. Subjects were asked to memorize it for a subsequent memory test. In the retention period, a visual search display was presented for 600 ms and subjects reported the orientation of the target 'T' (an upright 'T' or an inverted 'T'). The memory cue either indicated the target location (valid) or not (invalid). In the memory test display, subjects reported the side of the original memorized color within the same color category. **b** Mean reaction times (RTs) and accuracies are shown for the 13 subjects across different conditions (error bars show SEM, the color bars in the right panel show the RT trend lines of each subject) (*$p < 0.05$, **$p < 0.01$)

Data collection and preprocessing

Behavioral data were recorded with E-prime 1.0 software, while EEG signals were collected using a 128-channel EGI system referenced to the Cz (129th) electrode site. The sampling rate was 1000 Hz, and the online bandpass filter was 0.1–48 Hz. Data were re-referenced against the average of all channels. An FIR 0.1–30 Hz bandpass filter was applied. ERPs waveforms were extracted by segmenting epochs from 200 ms before the onset to 1000 ms after the onset of the search displays. Channels with amplitude exceeded 200 µV were marked as bad and replaced through the interpolation of neighboring electrodes, and about 6 ± 6 channels were removed on average (mean ± SD). Eye blinks and muscle artifacts were excluded by using independent component analysis (ICA) (EEGLAB toolbox), each characterized by scalp maps and time courses (Delorme and Makeig 2004). Finally, trials with amplitudes exceeding 100 µV or with HEOG (horizontal electrooculogram) exceeding 30 µV were excluded. The ERPs were baseline corrected to the 200 ms pre-onset of search display and separated according to experiment conditions. For the search-related waveforms, a mean of 157 ± 11, 81 ± 5, 149 ± 8 and 77 ± 4 trials remained across subjects for valid and correct WM, valid and incorrect WM, invalid and correct WM, and invalid and incorrect WM conditions, respectively (mean ± SD). To balance the trial numbers of four conditions, we selected the trials with equal numbers for each condition for each subject randomly for the following analysis. One participant's data were excluded due to excessive blinking and other artifacts.

Behavioral data analysis

The mean accuracy during the search task and the mean reaction time (RTs) of the correct search trials were evaluated with a 2 (valid, invalid) × 2 (correct WM, incorrect WM) repeated measure analysis of variance (ANOVA). All statistical analysis was performed using SPSS Statistics Release 19 (IBM, Somers, NY, USA).

ERP analysis

Based on previous studies (Eimer et al. 2011; Hilimire et al. 2011; Kiss et al. 2012), the N2pc and SPCN analyses were focused on two topographical regions of interest (ROIs), including six electrodes around PO7 and six electrodes around PO8. This method can effectively improve the signal to noise ratio (Gosling and Astle 2013; Oemisch et al. 2017). The average waveforms were computed separately for each condition (valid and correct WM, valid and incorrect WM, invalid and correct WM, invalid and incorrect WM) and laterality (contralateral vs. ipsilateral). By observing the grand-average waveforms obtained from the contralateral and ipsilateral ERPs to the target location, the N2pc and SPCN components were quantified as the mean amplitudes in the post-stimulus interval 250–300 ms and 350–550 ms, respectively. These values were submitted to a 2 × 2 × 2 ANOVA with validity (valid vs. invalid), WM maintenance (correct WM vs. incorrect WM), and laterality (contralateral vs. ipsilateral) as factors. Post hoc *t* tests with Bonferroni correction for multiple comparisons were applied when necessary. Linear regression models were used to evaluate the relationship between behavioral performance and ERP activity. Specifically, the N2pc amplitude and the SPCN amplitude were correlated with the mean search RT in each of the four conditions, respectively.

Results

Behavioral results

Subjects correctly reported the location of the memory cue with 65.79% mean accuracy. A two-way ANOVA of the search performance was performed with validity and WM maintenance as factors. We found a significant main effect for validity [search acc: $F\,(1, 12) = 8.523$, $p = 0.013$, $_{p}\eta^2 = 0.672$; search RTs: $F\,(1, 12) = 35.853$, $p < 0.001$, $_{p}\eta^2 = 0.844$], showing higher search accuracy and faster search RTs in the valid conditions compared to the invalid conditions (see Fig. 1b). A significant main effect for WM maintenance [$F\,(1, 12) = 10.525$, $p = 0.007$, $_{p}\eta^2 = 0.681$] was observed for the search RTs, which revealed faster search RTs in the incorrect WM conditions compared to the correct WM conditions. Moreover, a significant interaction between validity and WM maintenance [$F\,(1, 12) = 5.095$, $p = 0.043$, $_{p}\eta^2 = 0.587$] were observed for the search RTs. Post hoc *t* tests revealed faster search RTs in the valid and incorrect WM condition compared to the valid and correct WM condition [$t\,(12) = 6.574$, $p < 0.001$], but there was no significant difference between the two levels of WM maintenance for invalid trials [$t\,(12) = 0.498$, $p = 0.627$].

Event-related potential results

Figure 2 displays the grand-average lateralized ERPs recorded at left/right posterior ROIs, contralateral or ipsilateral to the lateralized stimuli for the four conditions, and the difference waveforms (i.e., contralateral − ipsilateral) of the lateralized ERPs in the valid and correct WM and the valid and incorrect WM conditions. Three-way ANOVA of N2pc amplitudes with validity (valid vs. invalid), WM maintenance (correct WM vs. incorrect WM), and laterality (contralateral vs. ipsilateral) as factors showed a significant main

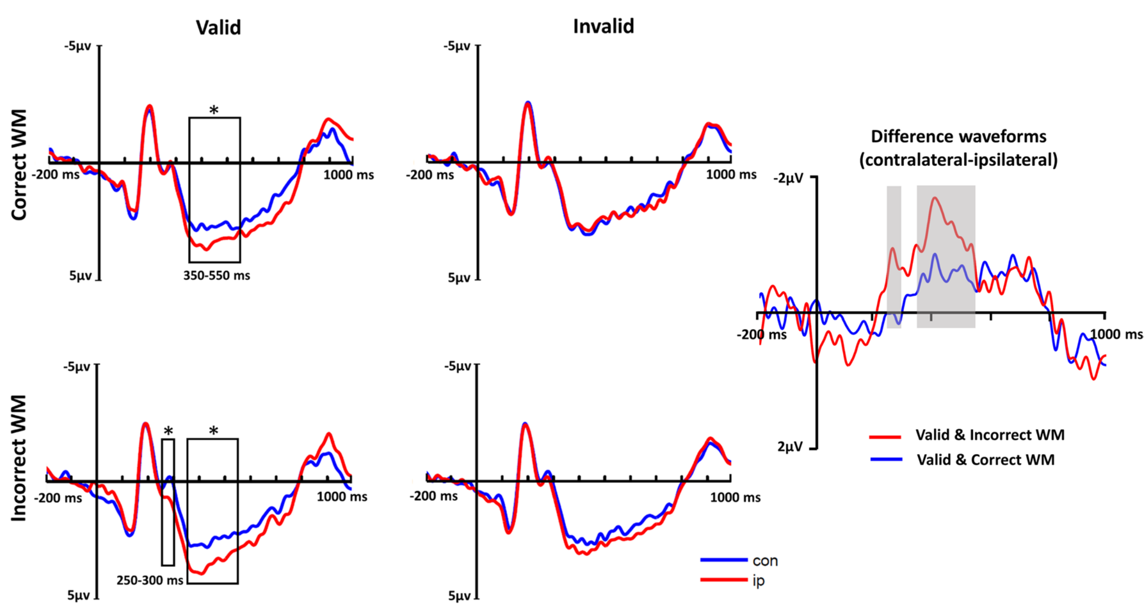

Fig. 2 Lateralized event-related potential (ERP) indices for search task at posterior electrode clusters. Activity is time locked to the onset of search display, for electrodes that are contralateral and ipsilateral to the target. Lateralized targets elicited an SPCN (350–550 ms) component in the valid trials. An N2pc (250–300 ms) component was observed in the valid and incorrect condition. The difference waveforms for the valid and correct WM and valid and incorrect WM conditions are shown in rightmost graph. Gray shaded rectangles show the time windows (250–300 ms, 350–550 ms) for statistical analyses

effect for validity [F (1, 12) = 8.044, p = 0.015, $_p\eta^2$ = 0.601], with a greater lateralized ERPs amplitude in the valid conditions relative to the invalid conditions. No significant main effects for WM maintenance and laterality were observed (all $p > 0.1$). The interactions between validity and laterality and between validity and WM maintenance were not significant (all $p > 0.1$). But the interaction between WM maintenance and laterality was significant [F (1, 12) = 5.583, p = 0.036, $_p\eta^2$ = 0.618], which indicated that the laterality was more pronounced in the incorrect WM conditions than in the correct WM conditions. Moreover, a significant 2 × 2 × 2 interaction [F (1, 12) = 4.974, p = 0.047, $_p\eta^2$ = 0.586] was observed, showing that the lateralized effect on N2pc was only detected in the valid and incorrect WM condition [F (1, 12) = 5.068, p = 0.044, $_p\eta^2$ = 0.597], but not in the other three conditions (all $p > 0.1$).

Three-way ANOVA of SPCN amplitudes with validity (valid vs. invalid), WM maintenance (correct WM vs. incorrect WM), and laterality (contralateral vs. ipsilateral) as factors showed a significant main effect for laterality [F (1, 12) = 5.972, p = 0.031, $_p\eta^2$ = 0.582], with a smaller amplitude at the contralateral electrode sites relative to ipsilateral sites, reflecting the emergence of the SPCN. No significant main effects for WM maintenance and validity were observed, and the interaction between validity and WM maintenance was not significant (all $p > 0.1$). But the interaction between validity and laterality was significant [F (1, 12) = 9.253, p = 0.010, $_p\eta^2$ = 0.617], which indicated that the laterality was more pronounced in the valid conditions than in the invalid conditions. We observed a marginally significant trend for an interaction between WM maintenance and laterality [F (1, 12) = 4.641, p = 0.052, $_p\eta^2$ = 0.579], which indicated that the laterality was a little more pronounced in the incorrect WM conditions than in the correct WM conditions. Moreover, a significant 2 × 2 × 2 interaction was observed [F (1, 12) = 5.730, p = 0.034, $_p\eta^2$ = 0.632], showing that the SPCN component was recorded in the valid and correct WM [F (1, 12) = 7.263, p = 0.019, $_p\eta^2$ = 0.637] and valid and incorrect WM [F (1, 12) = 17.416, p = 0.001, $_p\eta^2$ = 0.602] conditions, but not in the other two conditions (all $p > 0.1$). Post hoc t tests revealed greater SPCN amplitudes (contralateral − ipsilateral) in the valid and incorrect WM condition compared to the valid and correct WM condition [t (12) = 2.578, p = 0.024].

Correlations between ERP and behavior

We analyzed the correlations between the posterior lateralized ERP components and the visual search RT in each of the four conditions, respectively. A positive correlation between the N2pc amplitude and the search RT (r = 0.592, p = 0.033; Fig. 3a), and a positive correlation between the SPCN amplitude and the search RT (r = 0.607, p = 0.028; Fig. 3b) were observed in the valid and incorrect WM condition, but not in the other three conditions (all $p > 0.1$).

Discussion

The present study extends previous studies to show that the attentional guidance from WM can be modulated by the resource interchange between WM and the search processes,

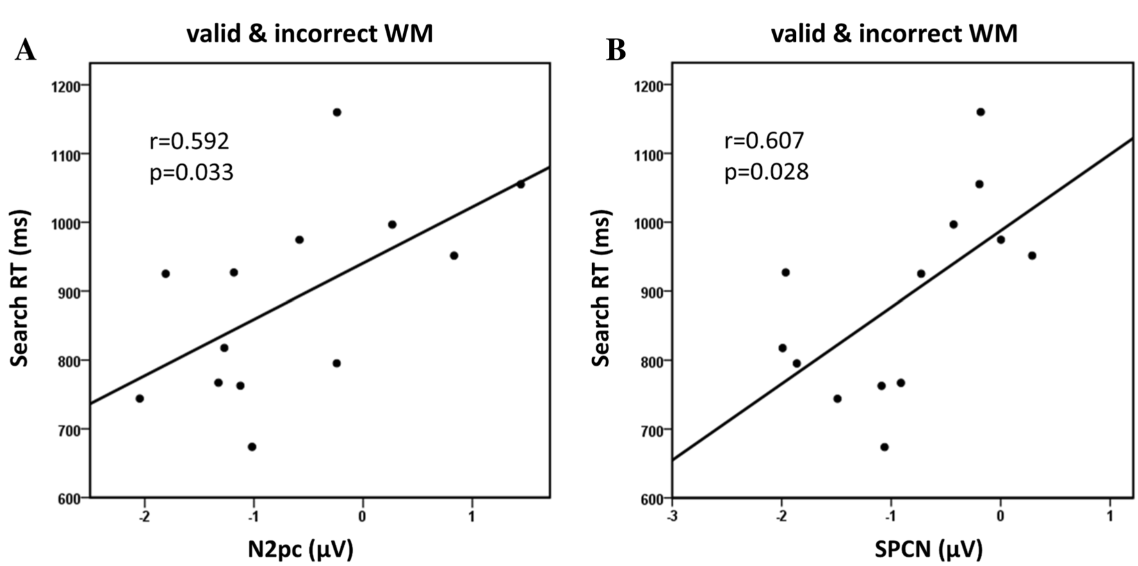

Fig. 3 Regressions between the posterior lateral ERP components and the search RT. **a** The N2pc amplitude is positively correlated with the search RT (r = 0.592, p = 0.033), and **b** the SPCN amplitude is positively correlated with the search RT (r = 0.607, p = 0.028) in the valid and incorrect WM condition

using ERP measures. Our findings show that search performance was facilitated in the valid relative to the invalid WM conditions. This is consistent with previous evidence showing that WM biases the competition for selection in favor of objects that fit the WM content (Huang and Pashler 2007; Hollingworth et al. 2013a). In the valid condition, efficient target selection was indicated by the lateralized components (Eimer et al. 2011; Mazza et al. 2011), while no lateralized components were observed in the invalid conditions wherein the memory cue and the search target did not share the same location (Mazza et al. 2011). These results are in line with that of Mazza et al. (2011), who proposed that the involuntary control that is driven by the irrelevant memory contents coexists with strategic mechanisms related to the target search, influencing attention selection with roughly equal power (Mazza et al. 2011). If the occurrence of the lateralized components reflects the joint contribution of the target and of the WM cue, it is likely that in the invalid condition these factors cancel each other's effect on attention capture and thus no lateralized components are observed.

The ERP results also revealed a differential effect of the valid correct vs. valid incorrect WM conditions on early (attentional selection) and later stages of processing (i.e., target stimulus identification). In the valid and incorrect WM condition, lateral targets elicited an N2pc component and a subsequent SPCN component. In the valid and correct WM condition, however, only an attenuated SPCN was observed. These results support the hypothesis that WM and visual search use the same set of processing resources (Woodman et al. 2007; Emrich et al. 2009), and compete with each other for more resources. Thus, when subjects did not actively attend to the memorized color during the maintenance interval, resulting in an incorrect response, more resources were available to the search task. This is indicated by an induced N2pc, reflecting attentional target selection (Eimer et al. 2009) and the allocation of attentional resources to the target stimulus (Mazza et al. 2009a), followed by an SPCN, reflecting more detailed processing of the target (Mazza et al. 2009b). Accordingly, the behavior shows a faster search response during the valid and incorrect WM trials. By contrast, when the cue was actively maintained in WM, less resources were available for the search task, resulting in a delayed (the search RTs were slower) and weakened attentional selectivity (reduced SPCN amplitudes) during the valid and correct WM condition in comparison with the valid and incorrect WM.

We found a positive correlation between the N2pc amplitude and the search RT and a positive correlation between the SPCN amplitude and the search RT in the valid and incorrect WM condition, suggesting that the greater the N2pc amplitude and the SPCN amplitude, the faster is the search RT. In addition, there was no significant correlation between the lateralized ERP components and the search RT for the other three conditions. These results imply that the ERP measure is consistent with the behavioral performance, both showing a further enhanced target selection processing in the valid and incorrect WM condition. However, in the other three conditions, such attentional guidance from WM was either reduced in the valid and correct WM condition or not shown in the invalid conditions.

In conclusion, the present study shows that WM attentional guidance is affected by the changes in the allocation of processing resources between WM and the visual search. The competitive interactions between WM and the visual search were more apparent in the valid relative to the invalid condition. This may imply that the memory content and the search target were processed concurrently in the valid condition, while this was not the case in the invalid condition. Future studies should consider using a smaller set size of the search display to reduce the complexity of the task, and a smaller percentage of the valid trials to prevent the subjects from strategically attending the WM-matching color to aid search.

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Author contributions MW, PY, ZLJ, JJZ and LL conceived and designed the experiments. MW and PY performed the experiments. MW and PY analyzed the data. MW wrote the main manuscript text. All authors reviewed the manuscript.

Compliance with ethical standards

Conflict of interest The authors declare that they have no competing interests.

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