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DISSOCIABLE MECHANISMS UNDERLYING INDIVIDUAL DIFFERENCES IN VISUAL WORKING MEMORY CAPACITY

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Highlights (3-5; maximum 85 characters, including spaces, per bullet point):

- High working memory capacity (WMC) is associated with better attention control.
- Mechanisms behind WMC-related differences in attentional control are not clear.
- We used frequency-tagging to track attention allocation to relevant and irrelevant information.
- Suppression of distractors is a key underlying mechanism for efficient attention control.

Abstract

Individuals scoring relatively high on measures of working memory tend to be more proficient at controlling attention to minimize the effect of distracting information. It is currently unknown whether such superior attention control abilities are mediated by stronger suppression of irrelevant information, enhancement of relevant information, or both. Here we used steady-state visual evoked potentials (SSVEPs) with the Eriksen flanker task to track simultaneously the attention to relevant and irrelevant information by tagging target and distractors with different frequencies. This design allowed us to dissociate attentional biasing of perceptual processing (via SSVEPs) and stimulus processing in the frontal cognitive control network (via time-frequency analyses of EEG data). We show that while preparing for the upcoming stimulus, high- and low-WMC individuals use different strategies: High-WMC individuals show attentional suppression of the irrelevant stimuli whereas low-WMC individuals demonstrate attentional enhancement of the relevant stimuli. Moreover, behavioral performance was predicted by trial-to-trial fluctuations in strength of distractor-suppression for high-WMC participants. We found no evidence for WMC-related differences in cognitive control network functioning, as measured by midfrontal theta-band power. Taken together, these findings suggest that early suppression of irrelevant information is a key underlying neural mechanism by which superior attention control abilities are implemented.

INTRODUCTION

Control of attention is critical for keeping behaviorally relevant goals active (e.g., replying to an important email) and inhibiting distractions (e.g., checking Facebook). The ability to control attention to minimize distraction has been suggested to be the primary factor determining an individual's working memory capacity (WMC; Kane et al., 2007), a characteristic that predicts a range of cognitive abilities, from stimulus processing (Brumback et al., 2004; Tsuchida et al., 2012) to fluid intelligence (Cowan et al., 2005; Engle et al., 1999). Behaviorally, high- compared to low-WMC individuals are less susceptible to visual (Hutchison, 2011; Kane and Engle, 2003; Unsworth et al., 2004) and auditory (Conway et al., 2001) distractions in tasks that require attentional control. For example, low-WMC individuals, more often than high-WMC individuals, notice task-irrelevant salient stimuli such as their own name (Conway et al., 2001), and are slower to inhibit automatic reactions to look towards unexpected visual stimuli (Unsworth et al., 2004). However, the strength of the relationship between WMC and attentional control seems to be task- and context-dependent (Heitz and Engle, 2007; Keye et al., 2013; Keye et al., 2009; Sorqvist et al., 2013; Wilhelm et al., 2013).

This frequently observed relationship between WMC and performance in attentional control tasks suggests that high- compared to low-WMC individuals are better able to suppress various sources of distraction. However, selective attention depends on two inter-related mechanisms: Suppression of irrelevant information and enhancement of relevant information (Andersen and Muller, 2010; Corbetta and Shulman, 2002; Gazzaley et al., 2005a; Polk et al., 2008). It is unknown whether WMC-related differences in attention control reflect differences in suppression of irrelevant information (Hasher et al., 2007), or enhancement of relevant information (Heitz and Engle, 2007), or a combination of both.

Indirect evidence for WMC-related differences in suppression of irrelevant information is provided by cognitive aging studies (Gazzaley et al., 2008; Gazzaley et al., 2005b). For example, Gazzaley and colleagues (2008) demonstrated age-related impairments in suppressing irrelevant information with no or weak changes in processing of relevant information. Moreover, they found that the decreased ability to suppress irrelevant information was related to impaired WM task performance, suggesting that the limited-capacity WM system was burdened with to-be-ignored irrelevant information. Although these findings may suggest that variations in WMC reflect differences in suppression of irrelevant information, cognitive aging effects are not limited to WM system, thus leaving the question about the neural mechanisms related to WMC open.

Fukuda and Vogel (2009) studied the relationship between WMC and attention control more directly by correlating WMC scores (as measured by change-detection task) with electrophysiological indices of attentional control. They reported WMC-related differences in early event-related potentials (ERPs) elicited by task-irrelevant probes at to-be-ignored locations, and interpreted such differences as a deficiency of low-WMC individuals to suppress distracting information. However, attention-related changes in early ERPs seem to reflect both suppression of irrelevant information and enhancement of relevant information (Couperus and Mangun, 2012), making it difficult to judge the relative contribution of these two processes in the Fukuda and Vogel (Fukuda and Vogel, 2009) results. Moreover, the WMC scores and electrophysiological indices of effectiveness of attentional control were derived from the tasks that share many features (e.g., multiple-stimulus arrays and short stimulus presentation times), thus raising concerns about the generalizability of the reported effects to other experimental contexts (cf., Mall et al., 2014), and calling for the need to investigate how attentional control is related to WMC using other typical WMC measures such as complex span tasks (Kane et al., 2004; Unsworth et al., 2005).

We addressed these limitations by recruiting high- and low-WMC individuals – defined in a separate session based on performance on two complex-span tasks – to perform a modified version of an Eriksen flanker task. By simultaneously presenting targets and flankers at different flicker frequencies to elicit frequency-specific steady-state evoked potentials (SSVEPs) we were able simultaneously to track attention allocation to the relevant and irrelevant information on a single trial level (Scherbaum et al., 2011). SSVEP amplitude is enhanced when an object or a specific feature is attended, and suppressed when it is unattended, compared to passive viewing of flickering stimuli (Andersen and Muller, 2010). We were thus able to determine whether better attentional control exhibited by high-WMC individuals is mediated by a stronger enhancement of relevant sensory information, suppression of irrelevant sensory information, or a combination of both.

An alternative explanation for WMC-related differences in sensitivity to the distracting information is that high- and low-WMC individuals might process stimuli differently in a later stage, during response-selection. Note that the two accounts – reduced sensory processing of distracting information in early stages and differences in response selection stage – are not mutually exclusive, and both might contribute to any observed differences in behavioral performance. Response selection and related action monitoring processes have been studied with EEG by focusing on oscillatory activity in theta-band (4-8 Hz; Cohen and Donner, 2013; Cohen and Ridderinkhof, 2013; Hanslmayr et al., 2008). Incongruent trials (e.g., EEFEE in the Eriksen flanker task), during which co-activation of competing action alternatives creates response conflict, are associated with increased theta-band activity in the frontal cognitive control network, which includes medial frontal and dorsolateral prefrontal areas (Cavanagh et al., 2009; Nigbur et al., 2012). Given that WM processes are related to theta-band activity in frontal networks (Hsieh and Ranganath, 2014), and that WM and conflict tasks engage overlapping fronto-parietal networks (Nee et al., 2007; Niendam et al., 2012), we hypothesized that high- and low-WMC individuals might differ in conflict-related theta. More specifically, we predicted that high-compared to low-WMC individuals would show smaller interference effects (difference between incongruent and congruent trials) in theta-band power.

MATERIALS AND METHODS

WMC screening

Six hundred and eighteen University of Groningen first-year psychology students performed Operation span and Symmetry span tasks in a separate experimental session at least 5 months prior to the Eriksen flanker task. Previous studies showed high test-retest reliability of complex span tasks, with correlations between sessions ranging from .70 to .83 (Klein and Fiss, 1999; Unsworth et al., 2005).

In the Operation span task (Unsworth et al., 2005), participants attempted to memorize 75 consonants that are serially presented in 3-7 item lists. Presentation of each letter is followed by an arithmetic problem. In the symmetry span task (Kane et al., 2004), participants attempt to memorize 42 spatial locations of serially presented red squares in a 4 × 4 grid, while judging the vertical symmetry of a pattern made up of black squares presented in an 8 × 8 grid. On each trial, locations and patterns were presented in 2-5 item lists.

The scoring procedure was done using a partial-scoring method (Conway et al., 2005), according to which correctly recalled items are given a partial credit if they are listed in the correct serial position even if all the items in the list are not recalled correctly. All list lengths (3 to 7 items in the operation span task and 2 to 5 items in the symmetry span task) were weighted equally and proportion of correct responses was computed for each list length separately (e.g., 2 of 5 = 0.4, 3 out of 3 = 1.0). Thus obtained proportions were averaged across all lists. Individual WMC scores in operation span and symmetry span tasks thus could range from 0 to 1. For each participant, a composite WMC score was computed by averaging normalized operation span and symmetry span scores.

Participants

As the goal was to characterize a specific dimension of individual differences rather than to estimate the exact effect size, an extreme-groups design was used (Yarkoni and Braver, 2010). Only participants whose composite WMC score fell in the upper (high-WMC group) and the lower (low-WMC group) quartiles of the distribution of composite WMC scores ($N = 618$, $Q1 = -0.41$, $Q3 = 0.60$ of z-WMC) were invited to the EEG session to perform the Eriksen flanker task.

To determine the required sample size to obtain adequate power, we used a previous report on WMC-related differences in early attention sensitive visual evoked potential (P150) while participants performed the Eriksen flanker task (Brumback et al., 2004). To achieve 80% power with a significance level of $\alpha = 0.05$, and an effect size of Cohen's d = 1.13 (calculated from the previous report; Brumback et al., 2004), the required number of participants per WMC group was 14 (t-test for differences between two independent means; Faul et al., 2007). However, as detectability of SSVEP amplitudes is also subject to individual differences (Fuchs et al., 2008), we collected more data than indicated by the power analysis.

Participants were 23 high-WMC individuals (z-WMC = 0.98, SD = 0.18) and 24 low-WMC individuals (z-WMC = -1.38, SD = 0.53). Data from 14 participants were excluded: One due to poor behavioral performance and four because their SSVEP responses were not higher than the general noise level. Exclusion of the remaining 9 participants was based on extensive eye-blink artifacts in more than 33% of all trials (range: 33-41%) that occurred during the critical pre-stimulus mask-to-response period. The fact that the pre-stimulus mask was presented for 1000 ms and an eye-blink can last for several hundred miliseconds meant that effective SSVEP entrainment was compromised on many trials. Note that in many other SSVEP studies, much longer stimulus presentation times are used (up to several seconds), making eye-blink artifacts less of a concern. Thus, 17 high-WMC (9 females, mean age 20.94, 4 left handed) and 16 low-WMC (14 females, mean age 21.31, 1 left handed) were included in the analysis. All participants had normal or corrected-to- normal vision. The study was conducted in accordance with the Declaration of Helsinki and approved by the local ethics committee. Informed consent was obtained from all participants.

Task

An Eriksen flanker task with a four-to-two mapping of stimuli to responses was used (Wendt et al., 2007). Stimulus presentation and response registration were controlled by a program written in Matlab using the Psychtoolbox library (Brainard, 1997). Stimuli were displayed on a 17-inch CRT monitor (1024 x 768 pixels; 100 Hz refresh rate). White stimuli comprised of a target letter and four identical flanker letters (two on each side of the target) were presented against a black background. The stimuli were presented in Sloan font, letters of which are equally discriminable and for which height equals width (Pelli et al., 1988). Viewing distance was 120 cm; each letter subtended 2.4° of visual angle, separated by 1.2° visual angle. Four letters (M, N, E, F) were mapped to two response keys. Speeded responses were to be made to the central target letter. Participants responded to the target letters M and E by pressing the "x" key with the left index finger and to N and F by pressing the ">" key with the right index finger. Only response congruent (e.g., M M M M M) and response incongruent (e.g., M M N M M) stimuli were used for the task. The overall probability of congruent and incongruent trials, as well as the proportion of left- and right-hand responses was kept equal. The task consisted of 50 practice and 640 experimental trials divided into 10 blocks with feedback (mean RT and accuracy) provided after each block. Participants were instructed to respond quickly while keeping accuracy levels around 90%. This was done to avoid ceiling effects in performance and minimize the effect of individual differences in speed-accuracy tradeoff settings.

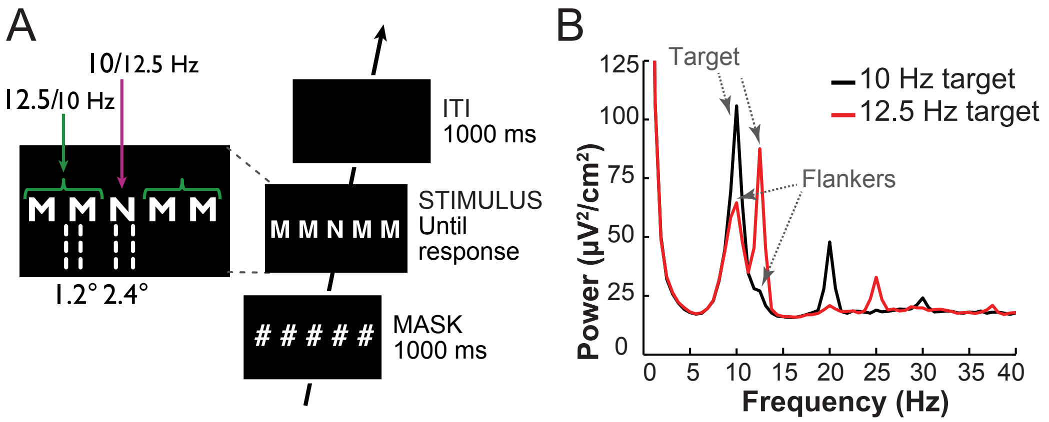

Figure 1. (A) Stimuli, task, and trial design. Modified version of the Eriksen flanker task showing an incongruent trial. Pre-stimulus mask (#####) and stimulus (MMNMM) were tagged with the same frequencies. (B) Frequency spectrum of the EEG signal averaged across all participants for the two frequency-tagging conditions: (1) 10 Hz target and 12.5 Hz flankers (black line), (2) 12.5 Hz target and 10 Hz flankers (red line). The subject-specific best-electrode was used in the plot.

Each trial started with a 1 s presentation of a pre-stimulus mask (# # # # #) with the central hash mark tagged with one frequency (e.g., 10 Hz) and the flankers with another (e.g., 12.5 Hz; see Fig. 1). Hash marks were then replaced by the stimulus (with tagging frequencies identical to the pre-stimulus mask period), which remained on-screen until the response was made or a deadline of 2 s was exceeded. The SSVEPs were elicited by modulating the brightness of the stimuli by a square wave (50% of the cycle on, 50% of the cycle off). Tagging frequencies of the target and flankers were reversed after each block.

Behavioral data analyses

The first trial of each block, error trials (incorrect or no-response trials), trials with RTs faster than 150 ms, and responses that fell outside 3 standard deviations of the mean were excluded from the RT data analysis. The RT thresholding procedure was performed separately for each participant, experimental condition (10 Hz and 12.5 Hz target), and trial type (congruent vs. incongruent). The differences between high- and low-WMC groups in behavioral performance were tested using repeated measures ANOVA with factors: Trial congruency (congruent and incongruent) and WMC group (high and low).

To quantify the evidence in favor of the "null effect" (non-significant results involving WMC group factor) by grading the decisiveness of the evidence (Jeffreys, 1961) we performed Bayesian analysis of variance (Rouder et al., 2012). Non-significant results involving the WMC group factor were subsequently evaluated by comparing Bayes factors of two models (with and without the WMC group factor) that were computed using *lmBF* function from package *BayesFactor* package in R (Morey and Rouder, 2013; Rouder et al., 2012). Comparison of Bayes factors of models allows assessment of the amount of evidence present in the data in favor of any hypothesis, including the null hypothesis, which is not possible with conventional analyses (Gallistel, 2009).

EEG recording and preprocessing

Sixty-two scalp EEG electrodes (Electro-cap International Inc., Eaton, Ohio, USA) were positioned according to the modified version of the international 10-20 system (6 additional electrodes were placed 10% below standard FT7, PO7, O1, FT8, PO8, and O2 electrode positions; F1, F2, CP1, CP2, FT7, and FT8 were not measured). Two additional reference electrodes were placed on the mastoids. Vertical and horizontal eye movements were recorded using four additional electrodes, two of which were placed below and above the left eye and the other two on the outer eye canthi. The data were recorded using an average reference REFA 8–72 amplifier (Twente Medical Systems, Enschede, The Netherlands). The data were digitally low-pass filtered at 140 Hz and sampled at 500 Hz. All offline data preprocessing and analysis was done using EEGLAB toolbox for Matlab (sccn.ucsd.edu/eeglab/) and custom written Matlab scripts.

The data were re-referenced offline to the average activity recorded at the mastoids and high-pass filtered at 0.5 Hz. Continuous EEG recording was epoched (-1 s to 3 s after pre-stimulus mask onset). The data were baseline corrected to the time window from -200 ms to the mask onset. Trials containing muscle artifacts or eye blinks during the time window of interest (the pre-stimulus mask onset to the response-execution) were manually removed. As it is common in SSVEP studies, the biggest proportion of rejected trials was due to eye blinks. The second step comprised of an independent component analysis, and components that did not account for any brain activity, such as eye movements (outside the time window of interest) or noise, were subtracted from the data. Extreme RT trials were also removed as described previously (see *Behavioral data analyses* section). The average number of trials per subject included in the analysis was 501.15 (*SD* = 49.84).

SSVEP analyses

Electrode selection. To select the appropriate electrode for SSVEP analysis, a subject-specific “best-electrode” approach was employed (Fuchs et al., 2008; Muller et al., 2003). For this purpose, artifact-free data were Laplacian transformed to increase topographical selectivity by filtering-out low spatial frequencies, which are considered to be a result of volume-conduction effects. Note that Laplacian transformation involves computation of the second spatial derivative, thus the units of EEG amplitude after transformation are μV/cm^2. Power (amplitude squared, μV^2/cm^2) at 10 and 12.5 Hz was estimated by FFT of the data in the time window from pre-stimulus mask onset to 600 ms post-stimulus (separately for the 10 Hz target and 12.5 Hz target conditions). These power estimates were used to calculate the attention effect (the power of 10 Hz flankers was subtracted from the power of 10 Hz targets, the same was done for the stimuli tagged with 12.5 Hz). The two thus obtained values were averaged for each channel and used to create iso-contour voltage maps. For each participant, the occipital electrode that showed the largest overall attention effect was selected for the analysis (Fig. 3C).

Computation of SSVEP amplitude. For the time-course analysis of SSVEP amplitudes, epoched data were concatenated (separately for 10 Hz and 12.5 Hz target conditions) to improve frequency resolution. Each time series was then filtered using narrow band-pass Gaussian filters with means of 10 and 12.5 Hz frequency and a standard deviation of 0.5 Hz. The filters were implemented by multiplying the FFT of the data by the exponential function:

$$e^{-0.5(f-f_0)^2/s^2},$$

where f is frequency, f_0 is the frequency of interest (10 and 12.5 Hz), and s is the specified standard deviation of the Gaussian, and then performing an inverse FFT. After filtering the data, the instantaneous amplitude at 10 and 12.5 Hz frequency was extracted using Hilbert transform. Subsequently, the epoched structure was recreated and averaged over trials. Trial average amplitude was baseline normalized to pre-mask period (-500 to -200 ms) by computing percent change of the amplitude at each time point relative to the average baseline interval amplitude. This normalization procedure was performed for two reasons: To remove scale differences between frequencies (power-law scaling) to allow comparison of 10 and 12.5 tagging frequency condition, and to eliminate scale differences between individuals allowing direct comparison between groups (Cohen, 2014; Roach and Mathalon, 2008). The relatively early baseline time window minimizes temporal leakage resulting from narrow filtering. Finally, baseline-corrected time series were averaged across 10 and 12.5 Hz conditions separately for targets and flankers.

Statistical analyses of SSVEP amplitudes. Two sets of statistical analyses were performed using a non-parametric cluster-based randomization procedure (Maris and Oostenveld, 2007). First, we assessed differences in target and flanker SSVEP amplitudes between WMC groups. Second, we compared changes in target and flankers SSVEP amplitude relative to the baseline separately for each WMC group.

In order to test our specific hypotheses concerning group differences in processing targets and flankers, the following steps were carried out for SSVEP amplitudes. First, independent samples t-tests were run comparing the SSVEP amplitude for high- and low-WMC groups at each time point from 0 to 1600 ms (where 0 is pre-stimulus mask onset). Second, a null hypothesis distribution was created at each time point by randomly assigning each participant to one of the two WMC groups, and t statistics were recomputed. This was repeated 500 times. Third, group differences in SSVEPs were considered statically significant if the actual t-value at that time point was greater than 95% of null t-values ($p < .05$, two-tailed). Fourth, cluster-based correction was applied to correct for multiple comparisons over time points. Clusters of contiguous time points were considered significant if the size of the cluster was bigger than expected under the null hypothesis at a significance level of $p < .05$. The null hypothesis distribution of cluster sizes was obtained by first thresholding the t-values obtained from each iteration of permutation testing at $p < .05$, and subsequently storing the maximum cluster size observed at that iteration step. Finally, to obtain more stable estimates from permutation testing we ran a “meta-permutation test” by repeating the permutation procedure 20 times. The averaged results from 20 permutations, each consisting of 500 iterations, are reported here.

Target and flankers SSVEP amplitude comparison against the baseline was performed following a similar procedure. First, four one-sample t-tests (separate for each condition and group) were run comparing the SSVEP amplitude for each time point in the time-window from 0 to 1600 ms (where 0 is pre-stimulus mask onset) against zero. Second, a null hypothesis distribution was created for each time point. This was done by taking the data from a random number of participants, multiplying by -1 (this converts baseline-minus-data to data-minus-baseline), and recomputing the t-values. The procedure was repeated 500 times, separately for each condition and each group. Third, changes in SSVEP amplitude relative to the baseline were considered statically significant if the actual t-value at that time point was greater than 95% of null t-values (i.e., $p < .05/4$, corrected for multiple comparisons across conditions and groups). Finally, cluster-based correction was applied to correct for multiple comparisons over time points, and permutation tests were repeated 20 times (each consisted of 500 iterations).

Control analyses. We used the tagging frequencies (10 and 12.5 Hz) within the alpha band (8-13 Hz) to acquire easily detectable SSVEPs, as high flicker frequencies produce small SSVEPs that are difficult to distinguish from the general noise level (Herrmann, 2001). However, suppression in the upper alpha-band (10-13 Hz) power over occipital, parietal, and frontal areas has been associated with active stimulus processing (Klimesch et al., 1998), and has been shown to differ between high and low IQ individuals (Doppelmayr et al., 2005; but see Toffanin et al., 2007). We therefore conducted additional analyses to test whether groups differed in endogenous task-related upper alpha suppression, to rule out an alternative interpretation of group differences in SSVEP amplitudes.

For upper alpha (10-13 Hz) power (amplitude squared) analysis the steps were identical to SSVEP amplitude computation, however a broader Gaussian filter with a mean of 11.5 and a standard deviation of 1 Hz was used to capture activity in the upper-alpha frequency range. The changes in alpha power are reported as percent change of the power at each time point relative to the pre-mask period (-300 to -100 ms). Statistical group comparisons in alpha-band power were performed using non-parametric cluster-based randomization procedure, as described previously (see *Statistical analyses of SSVEP amplitudes*).

Theta-band (3-7 Hz) power analyses

To extract theta-band activity, time-frequency decomposition was performed by convolving single-trial data from all electrodes with complex Morlet wavelets, defined as:

$$e^{i2\pi f_i t} e^{-t^2/(2\sigma^2)},$$

where t is time, f_i is frequency which ranged from 2 to 40 Hz in 40 logarithmically spaced steps, and σ is the width of each frequency band, which varied as a function of frequency ($4/(2\pi f_i)$) to obtain equally good frequency resolution at low and high frequencies. Instantaneous power was computed as the square of the complex convolution signal Z (*power* = $\text{real}[z(t)]^2 + \text{imag}[z(t)]^2$) and averaged across trials. Further, power values were normalized by converting to the decibel scale using the formula:

$$10\log_{10}(power/baseline),$$

where -300 to -100 ms pre-mask period served as a baseline.

Statistical analysis of theta-band power. The FCz electrode for theta-band power analyses was selected based on previous reports (Cavanagh et al., 2009; Cohen and Cavanagh, 2011a; Nigbur et al., 2012) and was confirmed by qualitative analyses (Figure 5A, the inset topographical maps). Because conflict-related brain activity is linked both to stimulus processing and to response preparation (Cavanagh et al., 2012), we separately tested changes in theta-band power time-locked to stimulus and response.

For stimulus-locked analysis, theta power values were averaged in a 300-650 ms time-window (where 0 is stimulus onset; Fig. 5A), and for response-locked analyses in a -200-100 ms time-window (where 0 is response; Figure 5C). Thus obtained power values were submitted to two separate repeated measures ANOVA with factors: Trial congruency (congruent and incongruent) and WMC group (high and low). Non-significant results involving WMC group factor were subsequently evaluated by comparing Bayes factors from ANOVA models using *BayesFactor* package in R, as previously described (see *Behavioral data analyses* section).

Single-trial analyses

To evaluate the effect of WMC-related differences in attention deployment to the target and flankers on the behavioral performance, we used linear mixed effects (LME) models with log RT as a dependent variable (Pinheiro and Bates, 2000). Logarithmic transformation of RTs was done to correct for positive skew of the RT distributions (Heathcote et al., 1991). LME models are extensions of standard regression models and allow modeling of single-trial data using both fixed effects (e.g., experimental manipulations) and random effects (e.g., inter subject variability) and thus account for both within- and across-subject variance. The modeling was implemented using *lmer* function from package *lme4* in R version 3.03 (Bates et al., 2014). The *p*-values were estimated for each factor of the fitted model using *lmeTest* package (Kuznetsova et al., 2013).

The best-fitting model selection was performed as follows. First, the base model was fitted, which included the fixed factors of WMC group, target flicker frequency, stimulus congruency, and single-trial SSVEP amplitude for target and flankers (averaged over stimulus-to-response window, no baseline correction applied) and interactions between the fixed factors. A random intercept term was included to account for participant-specific offsets. The categorical factors, such as WMC group (low and high), stimulus congruency (congruent and incongruent), and target flicker frequency (12.5 and 10 Hz) were dummy-coded to 0 and 1 (e.g., low-WMC was 0 and high-WMC was 1) before entering in models. Next, a model simplification procedure was performed by iterative removal of non-significant fixed effects and interactions while ensuring a stable goodness of the model fit by log-likelihood-based model comparison using χ^2 statistics (Baayen et al., 2008). We also examined whether the effect of target flicker frequency (10 or 12.5 Hz) had a different effect on the RTs of each participant. For this we included a random slope for target flicker frequency per participant, and compared if this improved the model fit. Following previous reports on positive relationship between RT and response-locked theta power (Cohen and Cavanagh, 2011a; Cohen and van Gaal, 2014) we also included in the model single-trial response-locked theta power (no baseline correction applied, averaged over -200 to 100 ms window) as an additional factor.

RESULTS

Behavioral performance

Despite the presence of the flicker, a typical congruency effect was observed (Fig. 2). Responses were faster ($F(1,31) = 35.48$, $p < .001$, $\eta^2_p = .53$) and more accurate ($F(1,31) = 7.49$, $p = .01$, $\eta^2_p = .20$) on congruent (510 ms; 7.2% error rate) than on incongruent trials (518 ms; 8.1% error rate). Consistent with previous reports (Heitz and Engle, 2007; Keye et al., 2009; Wilhelm et al., 2013), no statistically significant differences in reaction times (RTs) between high- and low-WMC individuals were observed ($F(1,31) = 0.78$, $p = .383$, $\eta^2_p = .03$). High-WMC individuals were numerically faster, and significantly less accurate ($F(1,31) = 8.10$, $p = .008$, $\eta^2_p = .207$). A follow-up analysis revealed that group differences in accuracy reflected that high-WMC individuals attained the instructed 90% accuracy requirement (one-sample *t*-test of error rate against 10 %: $t(16) = 0.72$, $p = .481$), whereas low-WMC did not ($t(15) = 5.86$, $p < .001$).

The size of the interference effects (measured as RT and accuracy differences on incongruent vs. congruent trials) did not differ between groups (RT: $t(31) = 1.38$, $p = .177$; accuracy: $t(31) = 0.41$, $p = .684$), corroborating previous findings when proportions of congruent and incongruent trials were kept equal (Heitz and Engle, 2007; Keye et al., 2009; Wilhelm et al., 2013). Because conventional ANOVAs do not allow for inferences supporting the null hypothesis (Gallistel, 2009), we performed a Bayesian ANOVA so that the strength of evidence in favor of the absence of an effect of WMC group could be evaluated (Rouder et al., 2012). We compared Bayes factors from a model with the main effect of congruency only with a full model including main effects of WMC group and congruency and their interaction. The evidence against including an interaction and the main effect of WMC on reaction times in the ANOVA model was 75:1, clearly indicating that groups did not likely differ in reaction time.

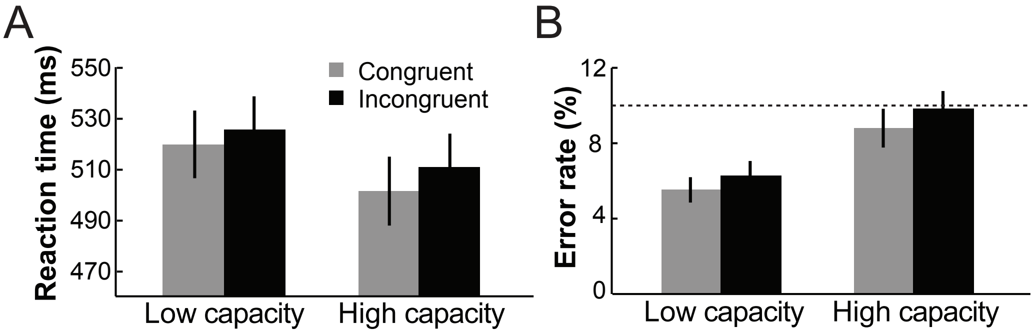

Figure 2. Behavioral results. Bars show reaction time (A) and error rate (B) as a function of working memory capacity. The error bars reflect one standard error of the mean. Dashed line in (B) denotes 10% error rate (the instructed performance level).

WMC-related differences in attention control

SSVEP amplitudes showed typical attention-related SSVEP effects when collapsing across both groups (Toffanin et al., 2009; Muller et al., 2003), such that SSVEP amplitudes were higher for the targets than for the flankers both for 10 Hz and for 12.5 Hz tagging frequencies (Fig. 1B). Furthermore, the topographical distribution of SSVEPs elicited by the flickering stimuli showed a maximum response at central occipitoparietal electrodes for the target, and at lateral electrodes for the flankers (Fig. 3A). Having demonstrated a typical attentional modulation of SSVEP amplitude, we further analyzed changes in SSVEP amplitude over time.

For both WMC groups, SSVEPs elicited by the central hash mark of the mask (i.e., the target position) showed an increase in amplitude relative to the pre-mask baseline period (-500 to -200 ms), an effect that was mirrored by a decrease in the amplitude for the flanking hash marks (Fig. 3B). These SSVEP amplitude differences during the pre-stimulus mask period continued into the stimulus presentation time. This pattern of results suggests that participants were focusing attention on the spatial location of the central item before and during the actual presentation of the target stimulus.

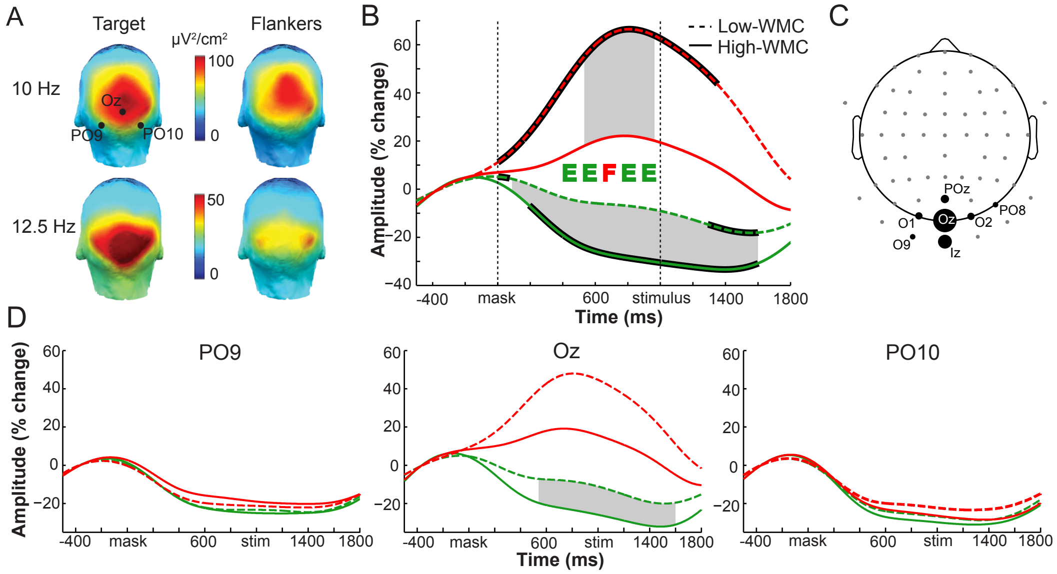

Figure 3. The effects of attention on the processing of target and flankers. (A) Topographical distribution of SSVEP power values (µV^2/cm^2) estimated by FFT of the data in the time window 0 to 1600 time-locked to the pre-stimulus mask onset. Plotted separately for target and flanker stimuli flickering at 10 and 12.5 Hz. (B) The time-course of SSVEP amplitudes for the target (red lines) and flankers (green lines) at the subject-specific best-electrode, averaged over two frequency-tagging conditions (10 Hz target and 12.5 Hz target, flankers tagged with 12.5 and 10 Hz respectively). Grey areas represent statistically significant differences between high- and low-WMC groups (corrected for multiple comparisons using cluster-based permutation testing), and black bolded lines represent statistically significant differences relative to the baseline (corrected for multiple comparisons using cluster-based permutation testing). (C) The distribution of electrodes used as a subject-specific "best-electrode" for SSVEP analysis. The size of the black circles indicates the relative frequency of the electrode used across participants: Oz (N = 15), Iz (N = 9), POz (N = 3); O1 (N = 2), O2 (N = 2), PO8 (N = 1), O9 (N = 1). (D) The time-course of SSVEP amplitudes for the targets and flankers at occipital electrodes (PO9, Oz, and PO10), demonstrating that group differences in the SSVEP amplitudes were observed only at occipital electrodes that showed strong SSVEP but were absent at electrodes that showed no clear SSVEPs (A).

The high- relative to the low-WMC group showed a significantly larger decrease in SSVEP amplitude for the flanking stimuli (all p values < .05 in the time interval 90 ms to 1600 ms after the mask onset, corrected for multiple comparisons using cluster-based permutation testing), whereas the low- relative to high-WMC group exhibited a stronger enhancement for the central stimulus (all p values < .05 in the time interval 540 ms to 970 ms after pre-stimulus mask onset, corrected for multiple comparisons using cluster-based permutation testing). Comparison of SSVEP amplitudes against the baseline revealed the amplitude of the target was significantly enhanced in the low-WMC group (all p values < .05 in the time interval 0 ms to 1350 ms after pre-stimulus mask onset, corrected for multiple comparisons using cluster-based permutation testing), whereas target SSVEP amplitude did not significantly differ from the baseline for the high-WMC group (Figure 3B). However, high-WMC individuals showed suppression of the flanking stimuli both during the pre-stimulus mask and stimulus presentation periods (all p values < .0125 in the interval 190 ms to 1600 ms after the pre-stimulus mask onset, corrected for multiple comparisons using cluster-based permutation testing). For the low-WMC group, flanker suppression was significant only during the imperative stimulus presentation time (1290 ms to 1600 ms).

Together these results show that although both low- and high-WMC groups attained relatively increased attention to targets compared to flankers, the groups used different strategies to obtain this signal-to-noise ratio: The low-WMC group increased attention to the target whereas the high-WMC group suppressed attention to the flankers.

Control analyses for SSVEP effects

Individual differences in endogenous task-related upper alpha suppression have been previously reported in studies comparing performance of high- and low-IQ individuals (Doppelmayr et al., 2005; but see Toffanin et al., 2007). To ensure that group differences in SSVEP amplitudes were not simply due to differences in upper alpha power, we conducted a series of additional analyses.

Although both groups showed topographically widespread upper alpha power suppression during the pre-stimulus mask and stimulus presentation (Fig. 4A), group differences in alpha were not statistically significant (all p values >.05 in the interval of interest from 0 ms to 1600 ms after the mask onset, corrected for multiple comparisons using cluster-based permutation testing; Fig. 4B). To quantify support for the null hypothesis, we compared Bayes factors from a model with WMC group as a fixed effect plus a random effect of participant identity and a model with only a random effect of participant identity only. Single-trial alpha power in a 0-1000 ms time window (no baseline correction applied) averaged over Oz, POz, and Cz electrodes was used as a dependent variable. The evidence in favor of including WMC group was 0.4:1, which slightly favors excluding this factor altogether, suggesting that any WMC-related differences in alpha power are negligible for the observed group differences in SSVEP amplitudes.

Moreover, statistically significant group differences in SSVEP amplitudes were constrained to occipital electrodes that showed strong SSVEPs (Fig. 3D); electrodes that showed no clear SSVEPs also showed no group differences, thus further supporting the interpretation that the changes in SSVEP amplitudes reported here reflect group differences in attention control rather than differences in alpha suppression.

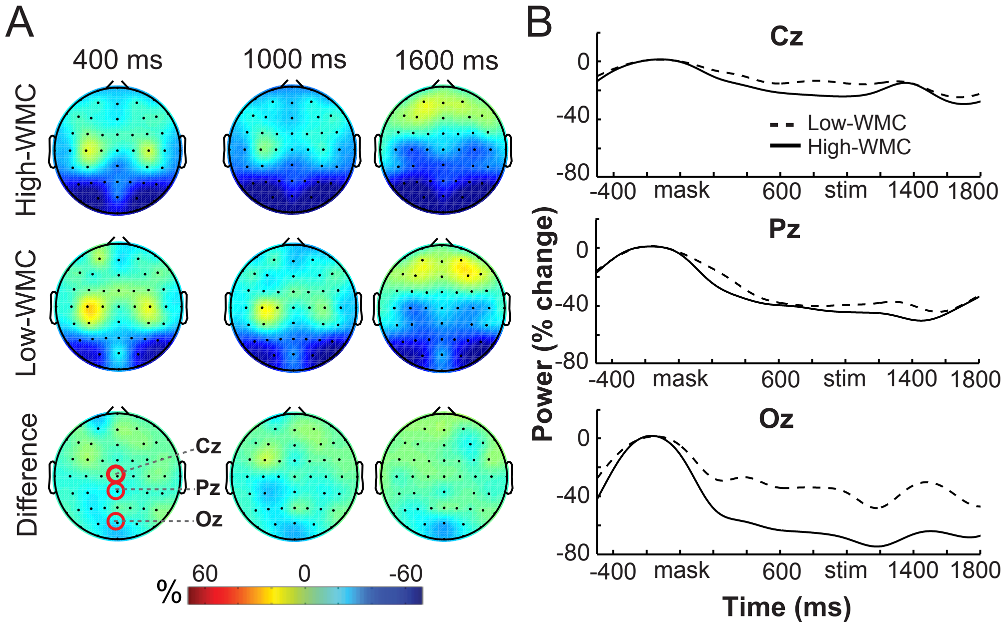

Figure 4. Topographical maps and the time-course of upper-alpha (10-13.5 Hz) power. (A) Each topographical map represents activity from the time point indicated in the graph ± 200 ms. (B) The time course of upper-alpha changes in power relative to the baseline period (-300 to -100 ms) in three scalp locations (Cz, Pz, and Oz). These data demonstrate that differences between high- and low-WMC individuals in SSVEPs were not due to differences in widespread endogenous alpha over occipital/parietal regions.

Conflict-related theta-band power

Theta-band power was increased compared to the baseline period in frontocentral sites for all conditions, with a spatial peak at the FCz electrode (Fig. 5A, C). Consistent with previous reports (Cavanagh et al., 2009; Nigbur et al., 2012), theta-band power was increased more for incongruent compared to congruent trials in both stimulus-locked (F (1,31) = 9.60; p = .004, η^2_p = .236) and response-locked (F (1,31) = 8.96; p = .005, η^2_p = .224) analyses. Although conflict-related changes in theta-band activity were evident for both high- and low-WMC individuals (Fig. 5B, D), no evidence for group differences in conflict processing were observed. The main effect of group was not significant ($F < 1$; for both stimulus- and response-locked analyses), nor was the Group x Trial type interaction ($F < 1$; for both stimulus- and response-locked analyses). We further performed a Bayesian ANOVA to compare the evidence in favor of the null hypothesis (a model with the main effect of congruency only) over the alternative (a full model including both main effects and an interaction). Bayes factor analysis showed that a model excluding an interaction with WMC was preferred at least 180:1 in the stimulus-locked analysis, and at least 161:1 in the response-locked analysis, providing strong evidence for absence of differences between high- and low-WMC groups in theta power.

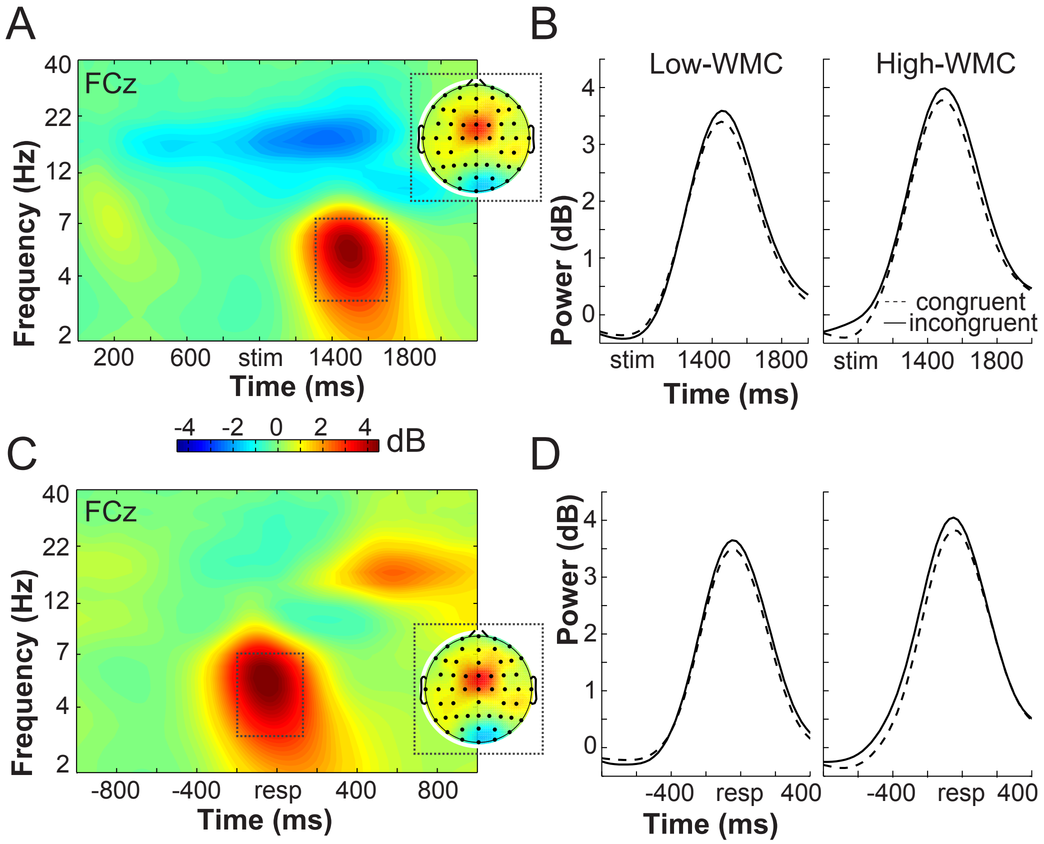

Figure 5. Time-frequency representation of a relative theta power (dB). (A) Stimulus-locked and (C) response-locked plots of relative to the baseline period (-300 to -100 ms pre-mask) power at FCz electrode. The inset topographical maps show mean theta-band (3-7 Hz) activity distribution over the scalp in time-frequency windows indicated by dashed squares: 300 to 650 ms for the stimulus-locked and -200 to 100 for the response-locked data. FCz electrode indicated by a black circle. (B) Stimulus-locked and (D) response-locked time-courses of theta-band (3-7 Hz) activity at FCz electrode for congruent and incongruent trials as a function of WMC group.

Single-trial analyses

Although group-level analyses revealed that high- and low-WMC participants differed in attention to the target and flankers, the exact contribution of target enhancement and flanker suppression on single-trial behavioral performance cannot be inferred from group-level results (Pernet et al., 2011). Therefore, we applied a linear mixed effects (LME) modeling approach to estimate the contribution of experimental parameters (fixed effects) and inter-subject sensitivity to experimental manipulations (random effects) on single-trial log RTs (Pinheiro and Bates, 2000). By means of a series of log-likelihood-based model comparisons (for details see Methods section), we derived an optimal model. Specifications of the model and statistics of the factors are reported in Table 1.

The strongest predictor for log RT was response-locked theta power, such that longer RTs were associated with higher theta-band power (β_{theta}). This effect was stronger for the high-WMC group ($\beta_{\text{theta x WMC}}$). The model also revealed that stronger suppression of the flankers was associated with longer RTs in the high-WMC but not in the low-WMC group ($\beta_{\text{SSVEP-Flanker x WMC}}$), although factors WMC group (β_{WMC}) and flanker SSVEP amplitude ($\beta_{\text{SSVEP-Flanker}}$) alone did not significantly predict log RTs. Moreover, log RTs were also affected by target flicker frequency ($\beta_{\text{Flicker-Target}}$), such that RTs were significantly slower when the target flickered at 10 Hz than when it flickered at 12.5 Hz. Finally, statistical analysis revealed that LME model with random slopes for target flicker frequency showed a significantly better fit compared to the model that included only random intercepts per participant (χ^2 (12) = 10.22, $p < .01$), meaning that there were individual differences in sensitivity to the flicker frequency.

Table 1. Specifications of the best-fitting LME model[*] and statistics

Fixed effects	***β***[**]	***df***	***t-value***	***p-value***
Participant (Intercept)	6.20	36	257	< .001
Theta	$1.93*10^{-9}$	16500	18.06	< .001
WMC [***]	$- 4.34*10^{-2}$	35	- 1.30	.202
Congruency[***]	$- 1.30*10^{-2}$	16470	- 5.01	< .001
Target flicker frequency (*Flicker-Target*)[***]	$1.72*10^{-2}$	35	4.76	< .001
Flanker SSVEP amplitude (*SSVEP-Flanker*)	$- 2.79*10^{-2}$	5437	- 1.51	.132
Theta x WMC [***]	$5.69*10^{-10}$	16510	3.45	< .001
Flanker SSVEP amplitude x WMC group[***]	$5.48*10^{-4}$	3648	2.34	.019
Random effects	***Variance***			
Participant	0.007			
Target flicker frequency (*Flicker-Target*)[***]	0.0002			

[*] RT ~ theta + WMC + congruency + Flicker-Target + SSVEP-Flanker + theta x WMC + SSVEP-Flanker x WMC + (1+Flicker-Target | Subject)

[**] Unstardandized β values are reported.

[***] Factors WMC group, stimulus congruency, and target flicker frequency are dummy-coded: Low-WMC = 0, high-WMC = 1, congruent = 1, incongruent = 0, 12.5 Hz = 0, and 10 Hz = 1.

DISCUSSION

This study provides direct electrophysiological evidence that WMC is related to the control of attention to both relevant and irrelevant information (Sauseng et al., 2009). In contrast to previous experimental designs that tested responses to relevant and irrelevant information in separate trials (Fukuda and Vogel, 2009, 2011; Gazzaley et al., 2008), we used an experimental approach that allowed us to track attention to relevant and irrelevant information simultaneously within trials. This approach revealed that high-WMC as compared to low-WMC individuals express stronger inhibition of irrelevant information while preparing for the upcoming stimulus, whereas low-WMC individuals enhance the relevant information more, possibly to compensate for deficient distractor suppression. Single-trial analyses showed that behavioral performance was predicted by trial-to-trial fluctuations in distractor suppression during the stimulus-response period for high-, but not for low-WMC participants. Taken together, these findings suggest that the ability to suppress irrelevant information is the key underlying neural mechanism by which superior attentional control abilities are implemented. Importantly, as average behavioral performance was similar for the two groups, the differences in neural dynamics reported here cannot be attributed to group differences in behavioral performance.

These individual strategic differences not only clarify the mechanisms behind more proficient attentional control often exhibited by high-WMC individuals (Kane and Engle, 2003; Vogel and Machizawa, 2004; Vogel et al., 2005), but also suggest an explanation for the weak or non-existent relationship between WMC and behavioral performance in some attention-demanding tasks that challenge attention control abilities (e.g., Heitz and Engle, 2007; Keye et al., 2009; Morey et al., 2012; Wilhelm et al., 2013). Namely, although individual differences in control of attention affect performance in WMC tasks, they will not necessarily translate into differences in performance in other attention-demanding tasks, because inefficient suppression of irrelevant information can be countered by an attentional boost to relevant information. Thus, it appears that the same signal-to-noise ratio can be achieved either by suppressing distractors or by enhancing targets. These two strategies appear able to result in similar performance, yet enhancement of targets is likely to be less neurally efficient (Neubauer and Fink, 2009).

In addition to revealing WMC-related differences in the temporal dynamics of attention control, our findings provide new insights into the relationship between the availability of working memory resources and dispersion of the “Mexican-hat” shaped distribution of spatial attention (Muller et al., 2005). Specifically, earlier work has shown that alternating zones of attentional facilitation and suppression are wider in low- than in high-WMC individuals, and even more dispersed after an increase in working memory load (Ahmed and de Fockert, 2012). Our finding of stronger suppression of distractors by high- as compared to low-WMC individuals suggests that efficient suppression may be the mechanism underlying the more focused profile of spatial attention in high-WMC individuals.

In the adaptation of the Eriksen flanker task used in the current study we replicated the conflict-related increase in theta-band power (3-7 Hz) reported in a classical version of the Eriksen flanker task (Cavanagh et al., 2009; Cohen and Cavanagh, 2011b; Nigbur et al., 2012). Single-trial analyses further demonstrated the validity of the current task as a test of cognitive control network function, as reaction times were strongly predicted by trial-to-trial fluctuations in theta power (Cohen and Cavanagh, 2011b). However, although previous reports of WMC-related differences in connectivity between DLPFC and other parts of the frontal cognitive control network (Cole et al., 2012; Faraco et al., 2011) might lead one to expect a relation between WMC and frontal midline theta, we did not find such differences. To our knowledge, the only other study to use EEG to examine WMC-related differences in conflict processing found group differences only in post-error brain activity (Miller et al., 2012). The failure to find group differences in theta power might also be related to the relatively long (1-s) foreperiod used in this experiment. Having a foreperiod might have resulted in similar priming of task-related functional brain regions for both WMC groups (Fassbender et al., 2006), thereby resulting in similar levels of conflict and absence of group differences in theta power.

The findings that high- and low-WMC individuals use different strategies to deal with distracting information have implications for attempts to use working memory training to increase general cognitive and intellectual abilities (Slagter, 2012). Specifically, our results suggest that training tasks that foster the cognitive process of inhibiting irrelevant information (Buschkuehl et al., 2012) would be more beneficial than tasks that aim for general working memory training.

Finally, our study has more general implications for the study of cognitive processes. Most SSVEP paradigms to date have used long-duration and large stimuli (e.g., Andersen and Muller, 2010; Muller et al., 2003; Toffanin et al., 2009), which suggests significant constraint on the types of cognitive processes that can be studied with SSVEP. In contrast, our finding of attentional modulation of a single target flanked by four salient distractors demonstrates that SSVEPs can be successfully applied to a variety of cognitive tasks, even those with small stimuli and relatively short presentation times.

To conclude, by simultaneously and independently measuring attention to the targets and distractors in a conflict task we reveal that high- and low-WMC individuals use different strategies to filter out distracting information. Specifically, high-WMC individuals focus on suppressing irrelevant information, whereas low-WMC individuals focus on enhancing relevant information. Because complex span tasks show high test-retest reliability (Engle, 2010; Unsworth et al., 2005), these strategic differences between high- and low-WMC individuals likely reflect stable trait-like mechanisms that affect perceptual processing of irrelevant information.

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