Inhibitory mechanisms involved in the retroactive orienting of attention within visual working memory: A neural oscillations perspective

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Abstract

Retroactive cuing of information after encoding improves working memory performance. However, there is an ongoing debate on the contribution of target enhancement vs. distractor inhibition attentional sub-processes to this behavioral benefit. We investigated the electrophysiological correlates of retroactive attentional orienting by means of oscillatory EEG parameters. In order to disentangle excitatory and inhibitory attentional processes, the to-be-memorized information was presented in a way that posterior hemispheric asymmetries in oscillatory power could be unambiguously linked to lateral target vs. distractor processing. Alpha power (8-13 Hz) asymmetries were insensitive to the number of cued or non-cued items, supporting their relation to the spatial orienting of attention. Furthermore, we found an increase in posterior alpha power contralateral to the position of non-cued working memory content that differed reliably from the alpha asymmetry in a neutral control condition. This correlate of an inhibitory sub-process of the spatial orienting of attention following the retroactive cues was further related to the participants' ability to control for the impact of irrelevant information on working memory retrieval. These findings indicate that shifting the spatial focus of attention within working memory makes use of an inhibitory attentional mechanism for guaranteeing a target-oriented retrieval process.

Keywords

working memory; selective attention; neural oscillations; inhibitory control; proactive interference

1. Introduction

There is a dynamic and rich stream of visual information from the environment that we have to deal with simultaneously. This requires to focus on and keep track of those inputs that are behaviorally relevant and to filter out those that are not. At this point, selective attention becomes important: We are able to bias information processing in favor of task relevant information, either by enhancing mental representations of target stimuli or potentially by inhibiting inputs that are irrelevant (Desimone & Duncan, 1995). These attentional control processes can act in support of perception by proactively biasing information processing in favor of anticipated targets (Rihs, Michel, & Thut, 2009; Snyder & Foxe, 2010) or by reactively deploying attention towards stimuli identified as task-relevant (Hickey, McDonald, & Theeuwes, 2006; Moher & Egeth, 2012). In addition, attention can be retroactively deployed on the level of working memory contents, meaning the mental representations of stimuli that are held activated over the short-term in order to enable detailed analysis and categorization (Baddeley, 1996; Baddeley & Hitch, 1974; Cowan, 1999). The current investigation was designed to further clarify how attentional selection within this memory system is instantiated.

In general, attentional deployment is thought to function from two sides: Mental representations of stimuli with task-relevant features are enhanced, while irrelevant inputs might be inhibited. This leads to a relative advantage for relevant stimuli and guarantees their representation in processing instances engaged in higher-level cognition and behavioral control (Desimone & Duncan, 1995; Luck, Chelazzi, Hillyard, & Desimone, 1997). For example, research concentrated on investigating the contribution of target enhancement and distractor inhibition processes to attentional orienting in visual search (Gaspelin, Leonard, & Luck, 2015; Hickey, Di Lollo, & McDonald, 2009; Sawaki, Geng, & Luck, 2012). It could be shown that inhibitory attentional control mechanisms, reflected in the distractor positivity component (Pd) of the event-related potential of the EEG, can proactively prevent the allocation of attention to

salient-but-irrelevant visual stimuli, at least when inhibitory control could be based on experience with a certain stimulus feature (Awh, Belopolsky, & Theeuwes, 2012; Wang & Theeuwes, 2018).

However, with respect to mental representations already encoded in working memory, inhibition as a cognitive process independent from target enhancement might not be a requisite mechanism: Prior investigations have shown that working memory representations that are marked as irrelevant after encoding are subject to interference by new sensory inputs (Barth & Schneider, 2018; Makovski, Sussman, & Jiang, 2008; Schneider, Barth, Getzmann, & Wascher, 2017; Schneider, Barth, & Wascher, 2017) and possibly to a rapid decay (Pertzov, Bays, Joseph, & Husain, 2013; Williams, Hong, Kang, Carlisle, & Woodman, 2013). Unattended working memory contents are thus stored in a passive and more fragile representational state (Sligte, Scholte, & Lamme, 2008; Vandenbroucke, Sligte, & Lamme, 2011), supported by the observation that they are no longer reflected in ongoing neural firing rates within cortical sites typically associated with working memory storage (Rose et al., 2016; Stokes, 2015; Wolff, Jochim, Akyurek, & Stokes, 2017). If this is the case, is there really a need for inhibitory control mechanisms in the updating of working memory contents?

In the current investigation, we will argue that there is a contribution of inhibitory control processes to retroactive attentional orienting. First evidence for this assumption came from investigations that included an experimental manipulation of stimulus position in a way that allowed the unambiguous association of hemispheric asymmetries in the EEG signal to attentional processing of lateral working memory items (see also: Hickey et al., 2009; Woodman & Luck, 2003). This was done by displaying to-be-memorized stimuli above vs. below and left vs. right side of central fixation (i.e., non-lateralized vs. lateralized positions). Oscillatory power in the alpha frequency range (8-13 Hz) increased contralateral to the position of non-cued working memory content when non-lateralized items were indicated as relevant. Furthermore, alpha power decreased contralateral to the position of a cued memory item when the non-cued

item was presented above or below fixation (de Vries, van Driel, Karacaoglu, & Olivers, 2018; Schneider, Göddertz, Haase, Hickey, & Wascher, 2019). Importantly, we also manipulated cue meaning by cuing either the to-be-reported targets ('remember cues') or the irrelevant distractors ('forget cues'). Forget cues led to an earlier onset of the inhibitory process relative to conditions with cues indicating which item to remember. The other way around, remember cues led to on earlier onset of a contralateral alpha power decrease (reflecting target selection) than forget cues that only indirectly indicated target position (Schneider et al., 2019). These results thus suggested that target- and distractor-related attentional mechanisms are at least partly independent during the focusing of attention on the level of working memory contents.

We now extended this experimental design by furthermore including varying set-sizes of the memory arrays and a control condition with a neutral retro-cue for a clear interpretation of hemispheric asymmetries as correlates of distractor inhibition vs. target enhancement. As prior investigations linked posterior alpha asymmetries to the spatial orienting of attention (Bae & Luck, 2018; Hakim, Adam, Gunseli, Awh, & Vogel, 2019), they should be independent of the number of cued vs. non-cued working memory representations. We further expected to replicate our prior finding of an increase in posterior alpha power contralateral to non-cued working memory contents and a respective decrease in oscillatory power contralateral to the position of cued items. Importantly, as we assume the alpha power asymmetries to be strictly related to the retinal positions of the memory array items, we hypothesize that a neutral retro-cue will cause a suppression of alpha power contralateral to the position of the left vs. right memory item (the still relevant non-lateralized item will be equally represented within both visual hemispheres and thus not cause an asymmetric effect). Importantly, we further hypothesize an increase in alpha power contralateral to the non-cued item(s) that differs reliably from the hemispheric asymmetry in the neutral condition. This would be an indication of an inhibitory process for withdrawing the focus of attention from the position of irrelevant working memory content. An increased

suppression of contralateral alpha power relative to the neutral condition when selectively cuing the lateral item(s) would indicate the enhanced processing at target location.

In order to further assess the functional relevance of the hypothesized inhibitory control mechanism during retroactive attentional orienting, we related the hemispheric alpha power asymmetries to the impact of irrelevant working memory content on retrieval performance. Participants were instructed to compare the color of the cued working memory contents with a later memory probe (i.e., 'same' vs. 'different' response). When presenting the memory probe in a non-cued color, working memory contents only recently identified as irrelevant by means of the retro-cues should interfere with the retrieval process (i.e., proactive interference; Monsell, 1978; Whitney, Arnett, Driver, & Budd, 2001). More efficient inhibition of the (position of) non-cued working memory representations should accordingly be associated with reduced proactive interference. This would highlight a relation of inhibitory mechanisms reflected in posterior alpha lateralization in reducing an enduring influence of irrelevant working memory content on goal-directed behavior.

2. Materials and Methods

2.1. Participants

Twenty-four participants (62.5% female, M(age) = 23.5, SD = 2.78, range = 19-30) took part in the experiment. They received 10 € per hour or course credit for participation. All participants were right-handed as tested by means of a handedness questionnaire. None of the participants reported any known neurological or psychiatric disease and all had normal or corrected-to-normal vision. Additionally, color perception was validated with the Ishihara Test for Color Blindness. Before the beginning of the experiment, all participants gave informed consent after receiving written information about the study's purpose and procedure. The procedure was in accordance with the Declaration of Helsinki and approved by the local ethics committee at the Leibniz Research Centre for Working Environment and Human Factors.

2.2. Stimuli and procedure

The stimuli were eight colored discs (RGB values: red: 255-0-0; blue: 0-0-255; green: 0-255-0; yellow: 255-255-0; magenta: 255-0-255; cyan: 0-255-255; purple: 50-0-100; orange: 205-128-0; grey: 128-128-128; average luminescence = 53.6 cd/m^2) presented along with grey sensory filler items (144-144-144, 53.6 cd/m^2) on a dark-grey background (38-416-33, 15 cd/m^2). A 22-inch CRT monitor (100Hz; 1024 x 768 pixels) was used for stimulus presentation. Participants were seated with a 150 cm viewing distance to the screen.

During the entire duration of the trial, a central fixation cross was displayed on the screen. At the beginning of each trial, a memory array composed of two to four items was presented for 300 ms (see figure 1). The memory items were presented on the vertical meridian and on the horizontal meridian. The items were presented at only one of the vertical and one of the horizontal positions (i.e., above vs. below and left vs. right of fixation). When there were two adjacent items on the horizontal or vertical positions, they were presented on hypothetical circles with 1.25° and 2.5° radius. When there was only one item on the vertical or horizontal position, it was presented on a hypothetical circle with a radius of 1.875°. The positions opposite of the presented items in each memory array were filled with grey items. These non-colored items were defined as task-irrelevant and presented to minimize the sensory disbalance of the memory array.

Afterwards, the fixation point started to morph into the retro-cue after a delay of another 300 ms. The morphing took 800 ms and was done in order to ensure that participants kept fixating before retro-cue onset. The cues lasted for 200 ms and indicated the position of the to-be-probed working memory items. For memory arrays with two items, there was also a neutral retro-cue indicating both items as further on task relevant. The combination of set-sizes and retro-cues led to five conditions (set-size two with neutral cue, set-size two with one relevant and one irrelevant item, set-size three with one relevant and two irrelevant items, set-size three with two relevant

and one irrelevant item and set-size four with two relevant and two irrelevant items). The number of trials within these conditions was balanced and they appeared in random order.

A probe stimulus followed the retro-cues with an inter-stimulus-interval (ISI) of 800 ms. The participants had to indicate by button press if the colored probe had been presented on the memory-array position indicated by the retro-cue. There were three types of probe stimuli: cued probes (50% of all trials) when probe color had been presented on the cued position(s), non-cued or 'recent negative' probes (20% of all trials; condition nonexistent following the neutral cue) when probe color had been presented on the non-cued position(s) and new probes (30% of all trials) when probe color was not shown within the prior memory array. The inter-trial interval varied between 500 and 1000 ms. The experiment consisted of 1440 trials and twenty practice trials. The trials were presented in 8 blocks with 180 trials each. The blocks were separated by short breaks of around two minutes to prevent fatigue in the course of the experiment. The whole procedure took 2.5 to 3 hours, including the preparation of the EEG setup.

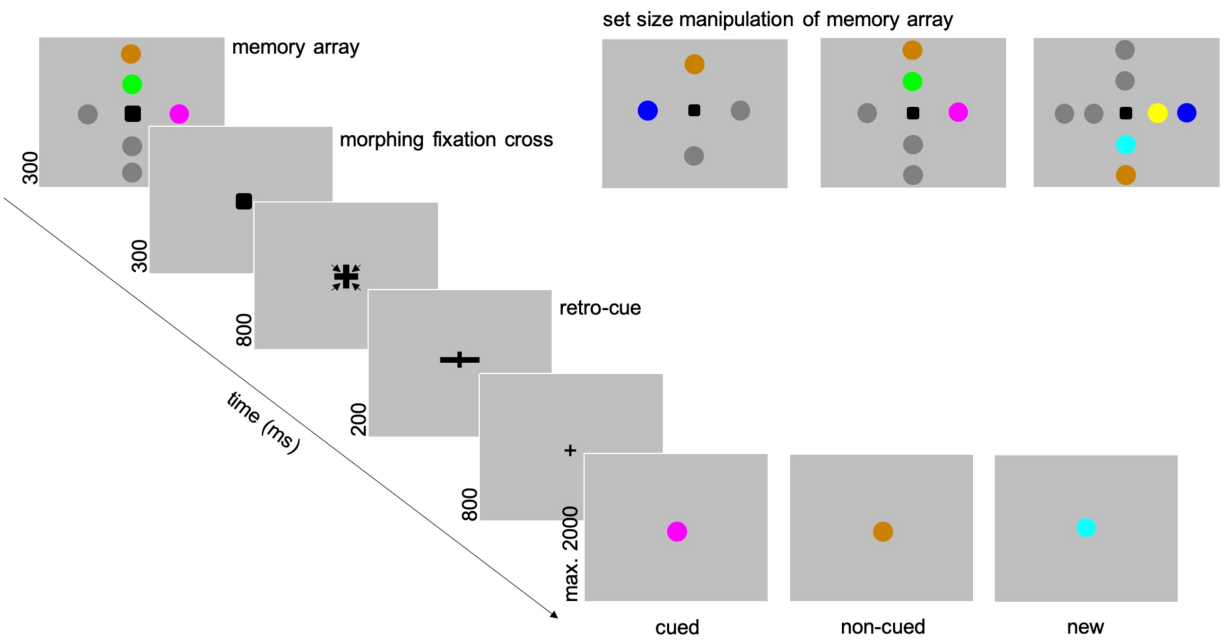

Figure 1. *Experimental design. A memory array differing in set size from two to four relevant (colored) items was followed by a retro-cue indicating either all (neutral condition; only for set-size two) or only the lateral vs. central items as task-relevant. The later probe display either contained a stimulus in color of (one of) the cued item(s), the non-cued item(s), or was presented in a color previously not included in the memory array.*

2.3. Behavioral analyses

Errors in the current experiment involved missed responses (no response within 2000 ms after probe presentation) and incorrect assignments of response categories. All responses prior to 150 ms after the onset of the memory probe were labeled as 'premature responses' and not included in the behavioral analyses.

First, we tested for differences in error rates and response times (RTs) within the conditions including selective retro-cues. Separate analyses of variance (ANOVAs) with the within-subject factors *'cued items'* (one vs. two) and *'non-cued items'* (one vs. two) were conducted. Analyses subsequently focused on the proactive interference effect by comparing RTs and error rates between the non-cued and the new probe condition. Repeated measures ANOVAs with the factors *'cued items'* and *'non-cued items'* further included a within-subject factor for *probe-type* (non-cued vs. new). Additionally, error rates and RTs were compared between conditions with selective vs. neutral retro-cues by means of two-sided within-subject *t*-tests (only for memory array set-size two).

2.4. EEG recording and preprocessing

EEG was recorded with a 1000 Hz sampling rate from 64 Ag/AgCl passive electrodes (Easycap GmbH, Herrsching, Germany) in extended 10/20 scalp configuration. A NeurOne Tesla AC-amplifier (Bittium Biosignals Ltd, Kuopio, Finland) was used for recording while applying a 250 Hz low-pass filter. Ground electrode was set to position AFz and FCz was used as online-reference. Channel impedances was kept below 10kΩ.

Data were analyzed using MATLAB® and the EEGLAB toolbox (Delorme & Makeig, 2004). High-pass (0.5 Hz, 0.25 Hz cutoff, 0 to -6 dB transition window) and low-pass filters (30 Hz, 33.75 Hz cutoff, 0 to -6 dB transition window) were applied and data were subsequently re-referenced to the average of all channels. Channels with kurtosis exceeding 5 SD (M=6 channels, SD=1.6) were replaced with a spherical spline interpolation of the immediately proximal

channels. In order to allow for a reliable identification of eye-movements within our data, this rejection method was not applied to the anterior lateral channels (F9, F10, AF7, AF8, AF3, AF4, Fp1, Fp2). Data were segmented into epochs from 1000 ms before to 3600 ms after presentation of the memory array. Independent component analysis (ICA) was run on every second epoch and ADJUST (Mognon, Jovicich, Bruzzone, & Buiatti, 2010) was used for detecting and removing components labeled as eye blinks, vertical eye-movements and generic data discontinuities. Additionally, single dipoles were estimated for each IC by means of a boundary element head model (Fuchs, Kastner, Wagner, Hawes, & Ebersole, 2002). ICs with a dipole solution with more than 40% residual variance were excluded from the signal. Trials with residual artifacts were rejected by means of an automatic procedure implemented in EEGLAB (threshold limit: 1000 µV, probability threshold: 5 SD, Max. % of trials rejected per iteration: 5%). These preprocessing steps led to the rejection of 327 trials on average (SD=91.36).

In an additional step, we excluded trials containing strong EEG correlates of lateral eye-movements. This was done by selecting the lateral frontal channels F9/F10 and then sliding a 100 ms time window in steps of 10 ms within an interval from memory array onset to the onset of the memory probes (2400 ms later). A trial was marked for rejection, if the change in voltage from the first half to the second half of at least one of these 100 ms windows at F9 or F10 was greater than 20 µV (Adam, Robison, & Vogel, 2018; Schneider et al., 2019). This led to an additional rejection of 0 to 194 trials (M=74, SD=62.839).

2.5. EEG time-frequency analyses

Event-related spectral perturbation (ERSP; see Delorme & Makeig, 2004) was computed by convolving complex Morlet wavelets with each EEG data epoch, with the number of wavelet cycles in the data window increasing half as fast as the number of cycles used in the corresponding fast-fourier transformation (FFT). This led to 3-cycle wavelets at lowest frequency (i.e. 4 Hz) and 11.25-cycle wavelets at highest frequency (i.e. 30 Hz). Respective

values were extracted for 200 time points and for 52 logarithmically arranged frequencies from 4 to 30 Hz.

2.5.1. Hemispheric asymmetries in oscillatory power

Time-frequency analyses of hemispheric asymmetries began with the calculation of oscillatory power at electrode locations contralateral and ipsilateral to the position of cued vs. non-cued working memory contents in data collapsed across all selective retro-cue conditions. Lateral posterior electrodes were chosen in accordance with earlier investigations (PO7/8, PO3/4, P7/8, P5/6; see Gould, Rushworth, & Nobre, 2011; Schneider et al., 2019). The contralateral minus ipsilateral differences of the distractor lateral and target lateral conditions averaged across all set-size conditions were statistically contrasted by means of within-subject *t*-tests for each time-frequency data point. As described above, cluster-based permutation statistics were applied for correcting for multiple comparisons. These analyses revealed a clear significant time-frequency cluster in alpha frequency range (8-13 Hz) following the retro-cues (450-780 ms; see figure 3A). Further ANOVAs were run based on this time-frequency range and included the within-subject factors *'cued items'* (one vs. two), *'non-cued items'* (one vs. two) and *'eliciting stimulus'* (cued vs. non-cued item(s) lateral). Additionally, the same time and frequency ranges were used for testing whether posterior asymmetries in the target lateral and distractor lateral conditions differed significantly from zero (one-sided tests for contralateral enhancement vs. contralateral suppression).

A comparable procedure was used for the neutral retro-cue condition. As we expected posterior asymmetries in this condition to be comparable to the target lateral condition (the central item following neutral cues should not elicit any asymmetric response), we first compared each time-frequency point in the contralateral minus ipsilateral difference between the distractor lateral condition (averaged across all set-size conditions) and the neutral condition and then applied cluster-based permutation statistics. These analyses revealed a significant cluster from around 8 to 13 Hz and 450 to 900 ms following the cues (see figure 3B). A subsequent one-

sided *t*-test was used for testing if the asymmetry in the neutral retro-cue was reliably different from zero within this time-frequency range.

Prior investigations further raised issues regarding a potential confound of hemispheric alpha power asymmetries following the retro-cues by prior lateral offsets in fixation position. This was due to the fact that already the memory array featured a lateral bias to the left or right side. We accordingly measured the contralateral vs. ipsilateral event-related potential (ERP) at frontal channels F9/10 relative to the position of relevant lateral memory array stimuli. Already the memory array caused a contralateral negativity at F9/10 with a peak in the grand average difference wave at 610 ms (averaged across conditions). Mean amplitudes per condition were measured within a 100 ms time window centered on this peak and within the 200 ms interval prior to retro-cue presentation. To assess if these lateral offsets in fixation prior to cue presentation might be related to the hypothesized alpha power asymmetries, we made use of repeated measures ANOVAs with *eliciting stimulus* and the number of cued and non-cued items as within-subject factors. Additionally, we included a covariate for lateral eye movements (measured as frontal ERP asymmetry in the two time windows across experimental conditions; see also: supplementary material in Schneider et al., 2019).

For all statistical analyses (behavioral and EEG data), Greenhouse-Geisser correction (indicated by Greenhouse-Geisser ε) was applied when sphericity of the data was violated. Partial eta squared (η^2_p) was used as an indicator of effect size for all ANOVAs. For post-hoc analyses, the false discovery rate procedure as indicated by Cramer and colleagues (Cramer et al., 2016) was used for correcting for cumulation of Type 1 error within the ANOVAs. In these cases, adjusted critical *p*-values (p_{crit}) are provided. Cohen's d_z was used as a measure of effect size for within-subject *t*-tests. The false discovery rate (FDR) procedure was used when post-hoc comparisons required correcting for cumulative Type 1 error (indicated as adjusted *p*-values or p_{adj} for *t*-test parameters).

2.5.2. Correlational analyses

We furthermore investigated if and to what extent the described oscillatory EEG effects were related to the participants' ability to control for the interference of non-cued mental representations on working memory retrieval processes (i.e., proactive interference). In this regard, the alpha power patterns were correlated in a between-subjects way with the proactive interference effect on RT level (based on Pearson correlation). Correlations were statistically assessed using permutation tests employing 50000 combinations, an approach which reduces sensitivity to outlier values. As a correlate for distractor inhibition, we made use of the relative increase in contralateral posterior alpha in the distractor lateral compared to the neutral condition. The time and frequency ranges for this analysis were based on the results of the cluster-permutation statistics described above (i.e., 8-13 Hz and 450-900 ms).

3. Results

3.1. Behavioral data

Error rates varied with the number of cued items, with lower rates when only one item was cued, $F(1,23)=48.169$, $p<0.001$, $p_{crit}=0.033$, $\eta^2_p=0.677$, and with the number of non-cued items, with lower error rates for one non-cued mental representation, $F(1,23)=48.701$, $p<0.001$, $p_{crit}=0.05$, $\eta^2_p=0.679$. Additionally, the *cued x non-cued* interaction was significant, $F(1,23)=24.367$, $p<0.001$, $p_{crit}=0.017$, $\eta^2_p=0.514$. Post-hoc analyses showed that error rates were lower when one of two items compared to one of three items was cued, $t(23)=-3.250$, $p_{adj}=0.004$, $d_z=-0.663$. This difference in error rates was larger when comparing the conditions with two cued items as a function of the number of non-cued items, $t(23)=-7.804$, $p_{adj}<0.001$, $d_z=-1.593$ (see figure 2). However, based on set-size two of the memory array, selective retro-cues did not significantly reduce error rates relative to the neutral cue condition, $t(23)=-0.893$, $p=0.381$, $d_z=-0.182$.

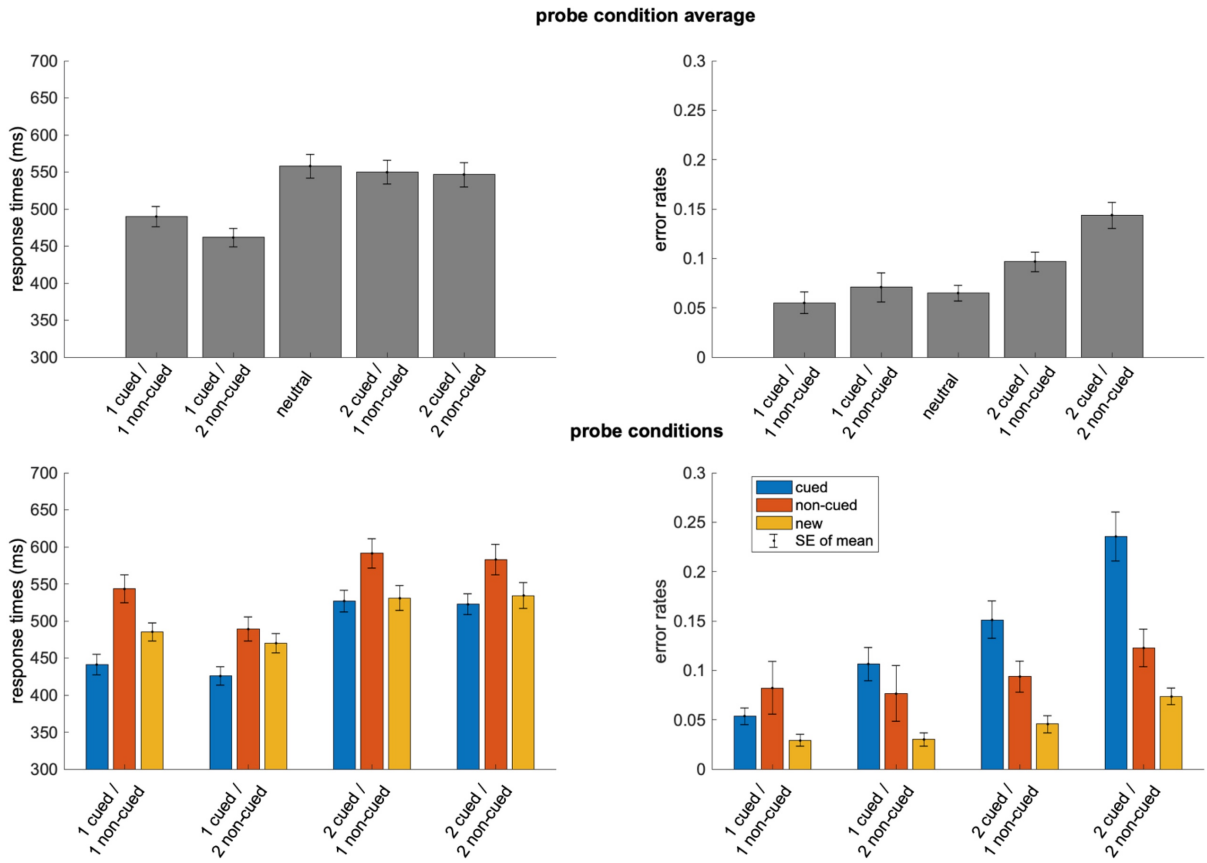

Figure 2. *Behavioral results. The upper plots show the response times (RTs) and error rates for the different retro-cue conditions, averaged across memory probe conditions. The lower plots depict response time and error rate patterns as a function of probe condition. The neutral condition was not displayed in this regard, as it did not include a non-cued probe condition.*

Further analyses concentrated on the comparison of the non-cued and new probe conditions. The non-cued probe condition featured generally higher error rates, $F(1,23)=7.613$, $p=0.011$, $\eta^2_p=0.249$. This effect was, however, not modulated by the number of cued or non-cued items (all F-values < 1).

RTs also varied with the number of cued items, $F(1,23)=97.035$, $p<0.001$, $p_{crit}=0.05$, $\eta^2_p=0.808$. Furthermore, RTs were faster with two non-cued items compared to one non-cued item, $F(1,23)=19.604$, $p<0.001$, $p_{crit}=0.017$, $\eta^2_p=0.460$, and there was a significant *cued x non-cued* interaction, $F(1,23)=20.014$, $p<0.001$, $p_{crit}=0.033$, $\eta^2_p=0.465$. Post-hoc t-tests indicated that RTs were faster when one of three items (1 cued / 2 non-cued) compared to one of two items (1 cued / 1 non-cued) was retroactively cued, $t(23)=5.044$, $p_{adj}<0.001$, $d_z=1.030$, while no such difference as a function of the number of non-cued items was evident within the conditions based

on a two-item retro-cue, $t(23)=0.983$, $p_{adj}=0.336$, $d_z=0.201$. Further information on the nature of this interaction becomes evident when comparing RTs between the non-cued and new probe conditions that both demanded the same type of response. In line with our hypotheses, the RT difference between these conditions was modulated by both the number of cued, $F(1,23)=6.918$, $p=0.014$, $\eta^2_p=0.231$, and the number of non-cued items, $F(1,23)=17.381$, $p<0.001$, $\eta^2_p=0.430$. Additionally, there was a trend toward a *cued x non-cued x probe-type* three-way interaction, $F(1,23)=3.951$, $p=0.059$, $\eta^2_p=0.147$. Further analyses indicated that the RT difference between the non-cued and new probe conditions was reduced when one of three items was cued (one cued / two non-cued), relative to the condition with one cued and one non-cued item, $F(1,23)=16.098$, $p<0.001$, $p_{crit}=0.017$, $\eta^2_p=0.412$. No such interaction was evident when comparing the conditions with two-item retro-cues as a function of the number of non-cued items, $F(1,23)=2.033$, $p=0.167$, $p_{crit}=0.033$, $\eta^2_p=0.081$. This suggests a more efficient handling of the proactive interference effect when the focus of attention could be limited to a single item after working memory resources had earlier been applied for the storage of three memory array stimuli (see figure 2). Additionally, RTs were faster following a selective retro-cue compared to a neutral cue within the set-size two condition, $t(23)=-7.149$, $p<0.001$, $d_z=-1.459$, indicating a general retro-cue benefit on RT level.

3.2. Hemispheric asymmetries in oscillatory power

As illustrated in figure 3, cluster-corrected comparisons between the target lateral and distractor lateral conditions (averaged across all conditions with selective retro-cues) revealed a latency interval with a reliable difference in alpha frequency range (8-13 Hz) from approximately 450 to 780 ms after retro-cue onset (see figure 3A). Follow-up analyses were focused on this time and frequency interval. As already indicated by the cluster-corrected *t*-tests, there was a main effect of eliciting stimulus, $F(1,23)=33.157$, $p<0.001$, $\eta^2_p=0.590$. This effect was composed of an increase in alpha power contralateral to the non-cued items, $t(23)=6.837$,

p_{adj}<0.001, d_z=1.396 (t-test against zero), and a contralateral alpha power suppression when cued items were presented at the lateral positions, $t(23)$=-2.341, p_{adj}=0.014, d_z=-0.478 (t-test against zero). As hypothesized, this effect was not modulated by the number of cued items, $F(1,23)$=2.877, p=0.103, η^2_p=0.111, or non-cued items, $F(1,23)$=0.307, p=0.585, η^2_p=0.013. Also the three-way interaction was statistically non-significant, $F(1,23)$=0.932, p=0.344, η^2_p=0.039.

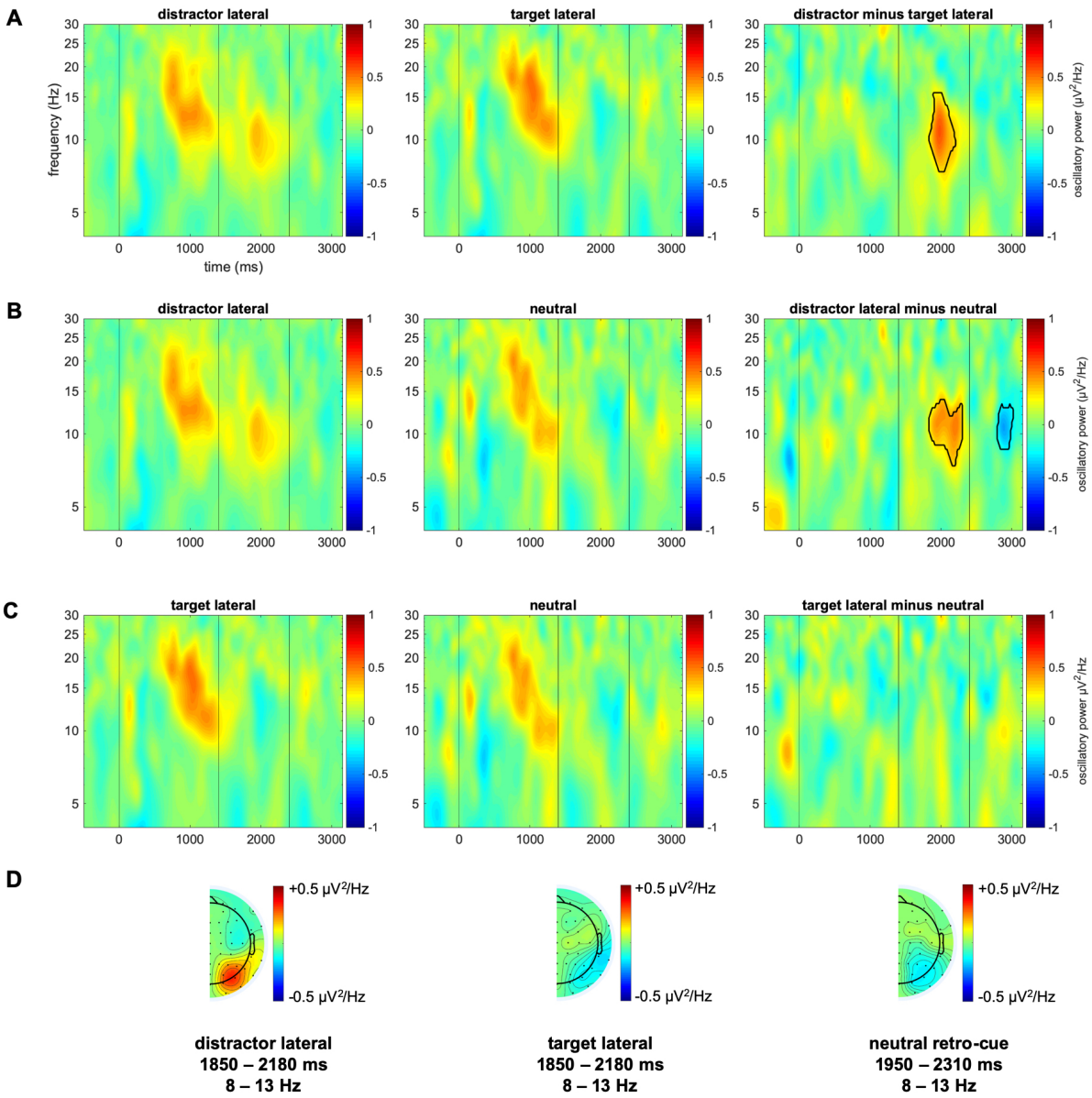

Figure 3. *Hemispheric asymmetries in oscillatory power. 3A depicts the comparison of the distractor lateral and target lateral contralateral-ipsilateral differences. The respective comparison of the distractor lateral and neutral conditions is shown in 3B. The comparison of the target lateral and neutral condition is depicted in 3C. Vertical lines indicate the onsets of the memory array, retro-cue and memory probe. The topographies of these effects (D) are only displayed on one hemisphere, because contralateral and ipsilateral signals are averaged across left- and right hemispheres.*

In a further step, we compared the neutral condition against the distractor lateral condition (averaged across memory array set-sizes) based on the cluster-correction procedure (see figure 3B). This again brought up a time-frequency area with a statistically reliable difference between conditions from 8 to 13 Hz and from 550 to 910 ms following the cues. When testing for a posterior asymmetry in alpha power based on these parameters, a contralateral suppression of alpha power in the neutral retro-cue condition was evident, $t(23)=-1.999$, $p=0.029$, $d_z=-0.408$ (*t*-test against zero). No statistically reliable difference was observed between the target lateral condition and the neutral condition (see figure 3C).

We furthermore assessed whether lateral eye movements following memory array and prior to retro-cue presentation had any influence on the difference of alpha power asymmetries between conditions with lateral targets vs. lateral distractors. In line with earlier findings objecting such a relationship (de Vries et al., 2018; Schneider et al., 2019), the ANCOVA with mean contralateral-ipsilateral difference from 560 to 660 ms at F9/10 as covariate still revealed a reliable difference in posterior alpha asymmetry following lateral targets vs. distractors, $F(1,22)=28.298$, $p<0.001$, $\eta^2_p=0.563$. The interaction of *eliciting stimulus* and the eye-movement covariate was non-significant, $F(1,22)=2.213$, $p=0.151$, $\eta^2_p=0.091$. The same results were found when measuring lateral eye-movements in the 200 ms interval prior to retro-cue onset, with a statistically significant effect of *eliciting stimulus* on alpha power asymmetries, $F(1,22)=33.604$, $p<0.001$, $\eta^2_p=0.604$, and a statistically non-reliable interaction, $F(1,22)=2.294$, $p=0.144$, $\eta^2_p=0.094$. This clearly shows that the asymmetric alpha modulations following the retro-cues cannot have been caused by prior systematic effects of lateral eye movements.

3.3. Correlational analyses

These analyses were run in order to relate the oscillatory correlates of retroactive attentional orienting to the extent of proactive interference by non-cued working memory representations. The latter was assessed as the difference in RTs between the non-cued and new probe conditions

and reflects to what extent non-cued mental representations interfere with target-oriented information processing following the retro-cues. The extent of the posterior increase in alpha power contralateral to the non-cued position (relative to the posterior asymmetry in the neutral retro-cue condition; see figure 3) reliably predicted the non-cued minus new probe difference on RT level (r=-0.462, p=0.003; see figure 4). Participants with a stronger distractor inhibition effect, measured as the difference in alpha asymmetry between the distractor lateral and neutral retro-cue conditions, thus revealed a reduced proactive interference effect. As a side note, this correlation slightly failed to reach statistical significance when not using the neutral retro-cue condition as a baseline for the alpha power increase contralateral to distractors (r=-0.288, p=0.108).

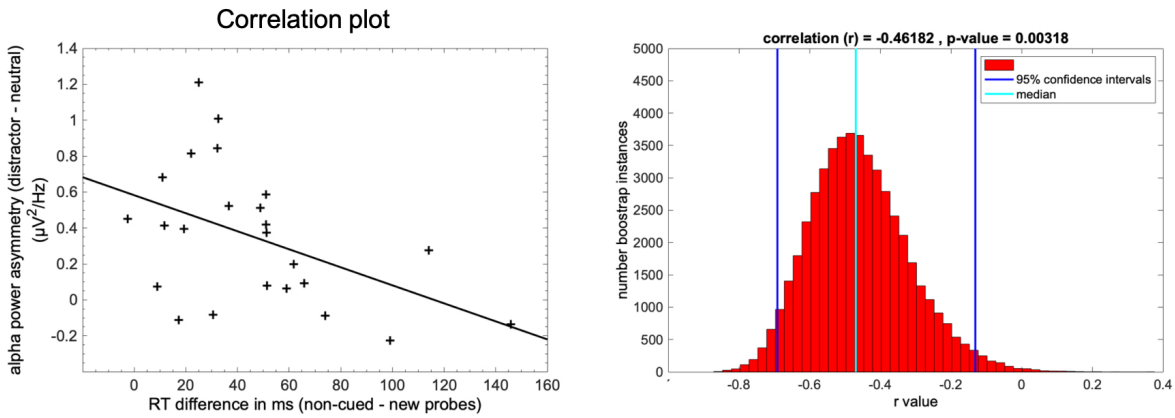

Figure 4. *EEG-behavior correlational results. The correlation was calculated for the difference in hemispheric asymmetries between the distractor lateral and neutral retro-cue condition (based on the significant cluster indicated in figure 3B). Correlations were statistically assessed based on permutation tests with 50000 combinations (see bar plot in the right part of the figure). A correlation can be considered as statistically significant when the 95% confidence intervals do not cross zero.*

4. Discussion

This study investigated if and how target selection and distractor inhibition processes are engaged during the attentional prioritization of information in working memory. This was done based on a paradigm that required dealing with the proactive interference of non-cued working memory contents during retrieval and memory probe processing. In line with earlier findings (Barth & Schneider, 2018; Makovski et al., 2008; Schneider, Barth, Getzmann, et al., 2017),

behavioral results showed a performance benefit for a one-item retroactive focus of attention (compared to two-item retro-cues) and a general retro-cue benefit compared to a neutral cue condition on RT level (Griffin & Nobre, 2003; Myers, Walther, Wallis, Stokes, & Nobre, 2015; Schneider, Mertes, & Wascher, 2015). These findings might be related to a special representational status of a single item within the focus of attention in working memory (Oberauer, 2002; Schneider, Barth, & Wascher, 2017).

Results further indicated that responding to a recently non-cued probe color entailed dealing with proactive interference, as both RTs and error rates were increased in this condition relative to a memory probe with a new color (see figure 2). Importantly, the proactive interference effect on RT level was reduced when only one item compared to two items was retroactively cued. The superior handling of the proactive interference effect resulted mainly from the one-item retro-cue condition including two non-cued items. This result pattern might be related to the fact that this condition featured the strongest release of attentional or working memory resources relative to the amount of resources applied during encoding and storage. This will in turn lead to a relatively stronger release of working memory or attentional resources following the retro-cues that might in turn be applied during probe processing.

The selective processing of working memory content has been associated with modulations of posterior alpha power (Hakim, Adam, Gunseli, Awh, & Vogel, 2019; Myers et al., 2015; Poch, Campo, & Barnes, 2014; Schneider et al., 2015; Schneider, Mertes, & Wascher, 2016). Here, we assessed retinotopic modulations of posterior alpha power by focusing on posterior hemispheric asymmetries (see figure 3). As hypothesized, alpha power lateralization was insensitive to the number of cued or non-cued working memory items, in line with its role in the spatial orienting of attention (Bae & Luck, 2018; Hakim et al., 2019). While this insensitivity of posterior alpha power asymmetries to the number of cued vs. non-cued items was already indicated by an earlier investigation (Poch, Carretie, & Campo, 2017), we further corroborate the notion that the spatial orienting of the focus of attention in working memory is based on

inhibition: As indicated in figure 3, hemispheric asymmetries in alpha power differed between conditions with lateral targets and lateral distractors. There was a contralateral suppression of posterior alpha power in the target lateral and neutral retro-cue conditions (see figure 3C). On the contrary, alpha power was increased contralateral to the positions of non-cued working memory content (compared to the ipsilateral grey stimuli that were defined as task-irrelevant already with memory array presentation). This distractor-related effect differed significantly from the neutral retro-cue condition, supporting the notion that retroactively updating the priorities of working memory contents is based on an inhibitory process for withdrawing attention from the non-cued position(s). Importantly, the alpha power response when selectively cuing lateral items did not differ from the neutral condition. This shows that withdrawing attention from irrelevant information does not likewise lead to a selective enhancement of attentional processing at the target location.

We furthermore observed a negative between-subjects correlation between the proactive interference effect and the oscillatory correlates of distractor inhibition. This relationship cannot simply be explained by a more suppressed representational quality of the non-cued information with increased contralateral alpha power. If hemispheric alpha power asymmetries reflected the selective remembering vs. forgetting of the non-spatial features stored in working memory (here: the color values), we would expect to also observe a modulation of this effect by the number of cued or non-cued colors. We thus propose that the inhibition of the non-cued position facilitates the selective retrieval of relevant information from working memory. In the current paradigm, selective working memory retrieval should involve a dissociation of the previously presented colors based on their spatial context (Oberauer & Kliegl, 2006). This color-location association should be less ambiguous when the non-cued positions have already been inhibited based on the retro-cue information.

In summary, we made use of an experimental task suited for assessing proactive interference as an indirect marker for the representational status of irrelevant working memory

representations. While the proactive interference effect on the level of task accuracy was not modulated by the number of cued or non-cued items, RT patterns indicated that the least interference by non-cued probe colors was evident when one out of three working memory items was retroactively cued. This might be related to the fact that this experimental condition allowed for the relatively highest amount of attentional or working memory resources to be re-engaged on memory probe processing following the retro-cues. However, hemispheric asymmetries in alpha power were not modulated by the number of cued or non-cued items and were thus unrelated to the selection/inhibition of non-spatial information content (here: representation of different color values). This finding is in line with the notion that posterior alpha power is related to the spatial orienting of attention (Bae & Luck, 2018; Hakim, Adam, Gunseli, Awh, & Vogel, 2019). Importantly, we showed that withdrawing the focus of attention from the position of lateral working memory content involved an inhibitory attentional control process (see figure 3A and 3B). This effect was related to the participants' ability to prevent proactive interference during working memory retrieval (see figure 4). Shifting the spatial focus of attention within working memory representations thus makes use of an inhibitory attentional mechanism, thereby guaranteeing a target-oriented retrieval process.

5. References

Adam, K. C. S., Robison, M. K., & Vogel, E. K. (2018). Contralateral Delay Activity Tracks Fluctuations in Working Memory Performance. *Journal of Cognitive Neuroscience, 30*(9), 1229-1240. doi:10.1162/jocn_a_01233

Awh, E., Belopolsky, A. V., & Theeuwes, J. (2012). Top-down versus bottom-up attentional control: a failed theoretical dichotomy. *Trends Cogn Sci, 16*(8), 437-443. doi:10.1016/j.tics.2012.06.010

Baddeley, A. D. (1996). Exploring the central executive. *The Quarterly Journal of Experimental Psychology Section A: Human Experimental Psychology, 49*(1), 5-28.

Baddeley, A. D., & Hitch, G. (1974). Working Memory. In G. H. Bower (Ed.), *The psychology of learning and motivation: Advances in research and theory* (Vol. 8, pp. 47-89). New York: Academic Press.

Bae, G. Y., & Luck, S. J. (2018). Dissociable Decoding of Spatial Attention and Working Memory from EEG Oscillations and Sustained Potentials. *J Neurosci, 38*(2), 409-422. doi:10.1523/JNEUROSCI.2860-17.2017

Barth, A., & Schneider, D. (2018). Manipulating the focus of attention in working memory: Evidence for a protection of multiple items against perceptual interference. *Psychophysiology*. doi:10.1111/psyp.13062

Cowan, N. (1999). An embedded-processes model of working memory. In A. Miyake & P. Shah (Eds.), *Models of working memory: Mechanisms of active maintenance and executive control* (pp. 62-101). New York, NY, USA: Cambridge University Press.

de Vries, I. E. J., van Driel, J., Karacaoglu, M., & Olivers, C. N. L. (2018). Priority Switches in Visual Working Memory are Supported by Frontal Delta and Posterior Alpha Interactions. *Cereb Cortex, 28*(11), 4090-4104. doi:10.1093/cercor/bhy223

Delorme, A., & Makeig, S. (2004). EEGLAB: an open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. *J Neurosci Methods, 134*(1), 9-21. doi:10.1016/j.jneumeth.2003.10.009

Desimone, R., & Duncan, J. (1995). Neural mechanisms of selective visual attention. *Annu Rev Neurosci, 18*, 193-222. doi:10.1146/annurev.ne.18.030195.001205

Fuchs, M., Kastner, J., Wagner, M., Hawes, S., & Ebersole, J. S. (2002). A standardized boundary element method volume conductor model. *Clin Neurophysiol, 113*(5), 702-712.

Gaspelin, N., Leonard, C. J., & Luck, S. J. (2015). Direct Evidence for Active Suppression of Salient-but-Irrelevant Sensory Inputs. *Psychol Sci, 26*(11), 1740-1750. doi:10.1177/0956797615597913

Gould, I. C., Rushworth, M. F., & Nobre, A. C. (2011). Indexing the graded allocation of visuospatial attention using anticipatory alpha oscillations. *J Neurophysiol, 105*(3), 1318-1326. doi:10.1152/jn.00653.2010

Griffin, I. C., & Nobre, A. C. (2003). Orienting attention to locations in internal representations. *J Cogn Neurosci, 15*(8), 1176-1194. doi:10.1162/089892903322598139

Hakim, N., Adam, K. C. S., Gunseli, E., Awh, E., & Vogel, E. K. (2019). Dissecting the Neural Focus of Attention Reveals Distinct Processes for Spatial Attention and Object-Based Storage in Visual Working Memory. *Psychol Sci, 30*(4), 526-540. doi:10.1177/0956797619830384

Hickey, C., Di Lollo, V., & McDonald, J. J. (2009). Electrophysiological indices of target and distractor processing in visual search. *J Cogn Neurosci, 21*(4), 760-775. doi:10.1162/jocn.2009.21039

Hickey, C., McDonald, J. J., & Theeuwes, J. (2006). Electrophysiological evidence of the capture of visual attention. *J Cogn Neurosci, 18*(4), 604-613. doi:10.1162/jocn.2006.18.4.604

Luck, S. J., Chelazzi, L., Hillyard, S. A., & Desimone, R. (1997). Neural mechanisms of spatial selective attention in areas V1, V2, and V4 of macaque visual cortex. *J Neurophysiol, 77*(1), 24-42. doi:10.1152/jn.1997.77.1.24

Makovski, T., Sussman, R., & Jiang, Y. V. (2008). Orienting attention in visual working memory reduces interference from memory probes. *J Exp Psychol Learn Mem Cogn, 34*(2), 369-380. doi:10.1037/0278-7393.34.2.369

Mognon, A., Jovicich, J., Bruzzone, L., & Buiatti, M. (2010). ADJUST: An automatic EEG artifact detector based on the joint use of spatial and temporal features. *Psychophysiology*. doi:10.1111/j.1469-8986.2010.01061.x

Moher, J., & Egeth, H. E. (2012). The ignoring paradox: cueing distractor features leads first to selection, then to inhibition of to-be-ignored items. *Atten Percept Psychophys, 74*(8), 1590-1605. doi:10.3758/s13414-012-0358-0

Monsell, S. (1978). Recency, Immediate Recognition Memory and Reaction Time. *Cognitive Psychology, 10*, 465-501.

Myers, N. E., Walther, L., Wallis, G., Stokes, M. G., & Nobre, A. C. (2015). Temporal dynamics of attention during encoding versus maintenance of working memory: complementary views from event-related potentials and alpha-band oscillations. *J Cogn Neurosci, 27*(3), 492-508. doi:10.1162/jocn_a_00727

Oberauer, K. (2002). Access to information in working memory: exploring the focus of attention. *J Exp Psychol Learn Mem Cogn, 28*(3), 411-421.

Oberauer, K., & Kliegl, R. (2006). A formal model of capacity limits in working memory. *Journal of Memory and Language, 55*(4), 601-626.

Pertzov, Y., Bays, P. M., Joseph, S., & Husain, M. (2013). Rapid forgetting prevented by retrospective attention cues. *J Exp Psychol Hum Percept Perform, 39*(5), 1224-1231. doi:10.1037/a0030947

Poch, C., Campo, P., & Barnes, G. R. (2014). Modulation of alpha and gamma oscillations related to retrospectively orienting attention within working memory. *Eur J Neurosci, 40*(2), 2399-2405. doi:10.1111/ejn.12589

Poch, C., Carretie, L., & Campo, P. (2017). A dual mechanism underlying alpha lateralization in attentional orienting to mental representation. *Biol Psychol, 128*, 63-70. doi:10.1016/j.biopsycho.2017.07.015

Rihs, T. A., Michel, C. M., & Thut, G. (2009). A bias for posterior alpha-band power suppression versus enhancement during shifting versus maintenance of spatial attention. *Neuroimage, 44*(1), 190-199. doi:10.1016/j.neuroimage.2008.08.022

Rose, N. S., LaRocque, J. J., Riggall, A. C., Gosseries, O., Starrett, M. J., Meyering, E. E., & Postle, B. R. (2016). Reactivation of latent working memories with transcranial magnetic stimulation. *Science, 354*(6316), 1136-1139. doi:10.1126/science.aah7011

Sawaki, R., Geng, J. J., & Luck, S. J. (2012). A common neural mechanism for preventing and terminating the allocation of attention. *J Neurosci, 32*(31), 10725-10736. doi:10.1523/JNEUROSCI.1864-12.2012

Schneider, D., Barth, A., Getzmann, S., & Wascher, E. (2017). On the neural mechanisms underlying the protective function of retroactive cuing against perceptual interference: Evidence by event-related potentials of the EEG. *Biol Psychol, 124*, 47-56. doi:10.1016/j.biopsycho.2017.01.006

Schneider, D., Barth, A., & Wascher, E. (2017). On the contribution of motor planning to the retroactive cuing benefit in working memory: Evidence by mu and beta oscillatory activity in the EEG. *Neuroimage, 162*, 73-85. doi:10.1016/j.neuroimage.2017.08.057

Schneider, D., Göddertz, A., Haase, H., Hickey, C., & Wascher, E. (2019). Hemispheric asymmetries in EEG alpha oscillations indicate active inhibition during attentional orienting within working memory. *Behav Brain Res, 359*, 38-46. doi:10.1016/j.bbr.2018.10.020

Schneider, D., Mertes, C., & Wascher, E. (2015). On the fate of non-cued mental representations in visuo-spatial working memory: Evidence by a retro-cuing paradigm. *Behav Brain Res, 293*, 114-124. doi:10.1016/j.bbr.2015.07.034

Schneider, D., Mertes, C., & Wascher, E. (2016). The time course of visuo-spatial working memory updating revealed by a retro-cuing paradigm. *Sci Rep, 6*, 21442. doi:10.1038/srep21442

Sligte, I. G., Scholte, H. S., & Lamme, V. A. (2008). Are there multiple visual short-term memory stores? *PLoS One, 3*(2), e1699. doi:10.1371/journal.pone.0001699

Snyder, A. C., & Foxe, J. J. (2010). Anticipatory attentional suppression of visual features indexed by oscillatory alpha-band power increases: a high-density electrical mapping study. *J Neurosci, 30*(11), 4024-4032. doi:10.1523/JNEUROSCI.5684-09.2010

Stokes, M. G. (2015). 'Activity-silent' working memory in prefrontal cortex: a dynamic coding framework. *Trends Cogn Sci, 19*(7), 394-405. doi:10.1016/j.tics.2015.05.004

Vandenbroucke, A. R., Sligte, I. G., & Lamme, V. A. (2011). Manipulations of attention dissociate fragile visual short-term memory from visual working memory. *Neuropsychologia, 49*(6), 1559-1568. doi:10.1016/j.neuropsychologia.2010.12.044

Wang, B., & Theeuwes, J. (2018). How to inhibit a distractor location? Statistical learning versus active, top-down suppression. *Atten Percept Psychophys, 80*(4), 860-870. doi:10.3758/s13414-018-1493-z

Whitney, P., Arnett, P. A., Driver, A., & Budd, D. (2001). Measuring central executive functioning: what's in a reading span? *Brain Cogn, 45*(1), 1-14. doi:10.1006/brcg.2000.1243

Williams, M., Hong, S. W., Kang, M. S., Carlisle, N. B., & Woodman, G. F. (2013). The benefit of forgetting. *Psychon Bull Rev, 20*(2), 348-355. doi:10.3758/s13423-012-0354-3

Wolff, M. J., Jochim, J., Akyurek, E. G., & Stokes, M. G. (2017). Dynamic hidden states underlying working-memory-guided behavior. *Nat Neurosci, 20*(6), 864-871. doi:10.1038/nn.4546

Woodman, G. F., & Luck, S. J. (2003). Serial deployment of attention during visual search. *J Exp Psychol Hum Percept Perform, 29*(1), 121-138.