Excitatory and inhibitory attentional mechanisms involved in the control of distractor interference in working memory: A neural oscillations perspective

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Abstract

Retroactive cuing of information after encoding improves working memory performance. It has recently been shown that this benefit is related to excitatory and inhibitory attentional sub-processes. We investigated the electrophysiological correlates of these mechanisms in a retroactive cuing task by means of oscillatory EEG parameters. In order to disentangle the processes related to distractor inhibition and target enhancement, the to-be-memorized information was presented in a way that posterior hemispheric asymmetries in oscillatory power could be unambiguously linked to target or distractor processing. Alpha power (8-13 Hz) following the retroactive cues increased contralateral to an irrelevant and decreased contralateral to the position of a relevant working memory representation. These effects were insensitive to the number of cued or non-cued items, supporting their role in spatial shifts of attention. Frontal theta power was increased for selective retro-cues compared to a neutral condition, but was also not modulated by the number of cued or non-cued items. It thus reflected the general need for higher-level attentional control in working memory. Non-lateralized posterior alpha and beta power prior to memory probe presentation was decreased for one compared to two cued items and for two compared to one non-cued item. Furthermore, alpha/beta power suppression in this time window was positively correlated to the interfering effect of irrelevant working memory contents on behavioral performance. Non-lateralized alpha and beta power decreases after retroactive cues might thus be a viable marker for the re-engagement of released working memory resources to support the control of distractor interference in working memory.

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, either by proactively biasing information processing in favor of anticipated targets (Rihs, Michel, & Thut, 2007; Sauseng et al., 2005; Snyder & Foxe, 2010; Worden, Foxe, Wang, & Simpson, 2000) or by reactively deploying attention towards stimuli identified as task-relevant (Beck, Luck, & Hollingworth, 2018; Gaspelin & Luck, 2019; 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 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 & Luck, 2010; for review: Gaspelin &

Luck, 2019). It could be shown that inhibitory attentional control mechanisms, for example 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; Failing, Wang, & Theeuwes, 2019; Gaspelin, Gaspar, & Luck, 2019; 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 at all 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, & Wascher, 2017) and possible 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, Akyürek, & Stokes, 2017). If this is the case, why then should working memory benefit from inhibitory control?

The answer is relatively simple. Information that is not actively stored can still significantly affect the amount of information that can be retrieved from working memory. This has been shown in investigations dealing with ‘proactive interference’ of previously relevant information in working memory paradigms (Atkinson & Juola, 1974; Monsell, Stephen, 1978; Whitney, Arnett, Driver, & Budd, 2001). It was shown that working memory contents from the previous trial interfered with retrieval when presented as a probe in the present trial (i.e., recent negative probes), leading to a decrement in response times and accuracy. In a similar way, we used this experimental procedure in a retroactive cuing (retro-

cue) working memory paradigm: Participants had to remember the color of four stimuli and were subsequently cued to focus only on the two stimuli presented to the left or right side of fixation. Afterwards, a single item was used as a memory probe and was presented in the color of either one of the cued items, one of the non-cued items (comparable to the 'recent negative probe' condition) or with a new color not used in the present trial. This also caused a decrement in response times for the non-cued probe condition relative to the new probe condition and this effect declined when the interval between the retro-cue and probe was extended. This indicates that proactive interference can be used as an indirect measure of the representational strength of irrelevant or passive working memory representations and that more time available for preparing for probe processing might benefit the control of this effect (Schneider, Mertes, & Wascher, 2015, 2016).

Here we made use of a modified version of this retro-cue paradigm to assess if and how target-related attentional processes and inhibitory control mechanisms are engaged to prevent or counteract proactive interference effects in working memory. A memory array contained either two, three or four differently colored discs at lateral (left vs. right of central fixation on vertical meridian) and central positions (below or above central fixation on horizontal meridian; see figure 1) and was followed by retroactive cues indicating the items at either of these positions as further on task relevant. Thus, the number of cued and non-cued items was manipulated independently (1 item cued / 1 item non-cued vs. 1 item cued / 2 items non-cued vs. 2 items cued / 1 item non-cued vs. 2 items cued / 2 items non-cued). Additionally, we implemented a neutral retro-cue without a selective bias towards any of the presented memory array items. The cues were followed by a central memory probe that resembled one of the items at the cued positions in 50% of all trials (demanding a 'positive' decision), but matched one of the items at the non-cued position (i.e., a 'recent negative probe' or non-cued probe) or was shown in a new color respective the prior memory array in the remaining trials (demanding a 'negative' decision).

If an active control process is engaged to prevent or counteract interference by non-cued contents, this process should depend on the amount of working memory resources available. We thus expect the performance decrement for non-cued relative to new probes to vary with the amount of working memory resources released following the retro-cues. In a comparable way, prior investigations revealed that retro-cue benefits depend on the amount of freed working memory resources, with increasing behavioral benefits for higher numbers of non-cued items (Myers, Walther, Wallis, Stokes, & Nobre, 2015; Nobre, Griffin, & Rao, 2008; Souza, Rerko, & Oberauer, 2014; Vandenbroucke et al., 2011; for review: Souza & Oberauer, 2016). Referred to the current experiment, this amount should vary with both the number of cued and non-cued items. For example, the strongest release of working memory resources is expected when three items were encoded, but retro-cues later indicated two items as task-irrelevant (2/3 of the initially engaged resources). Therefore, this experimental condition should feature the lowest proactive interference effect on behavioral level.

We further used oscillatory parameters of the EEG for assessing the sequence of target- and distractor-related attentional processes following the retro-cues. In this regard, frontal midline oscillatory power in theta range (4-7 Hz) was related to the detection of a need for attentional control mechanisms in a given task (Cavanagh & Frank, 2014). Referred to the current investigation, theta power should increase following selective retro-cues that demand an updating of working memory representations compared to neutral cues. Furthermore, theta power should vary with the demands on cognitive control mechanisms regarding the compensation for proactive interference. A preparatory engagement of cognitive control mechanisms would be evident following the retro-cues, while a compensatory application of cognitive control to prevent proactive interference would show up only after presentation of the memory probes.

While these oscillatory parameters reflect higher-level attentional control mechanisms, attentional orienting itself was shown to be represented in modulations of posterior alpha

power (7-14 Hz; Myers et al., 2015; Poch, Campo, & Barnes, 2014; Schneider et al., 2015, 2016). We manipulated stimulus position in a way that allowed the unambiguous association of hemispheric asymmetries to attentional processing of lateral items (Hickey et al., 2009; Woodman & Luck, 2003). Prior investigations have shown that when indicating a lateral item as irrelevant, this leads to a contralateral increase in posterior alpha power as a marker for inhibition of the non-cued stimulus position. Orienting attention toward a lateral target position is in turn reflected in a contralateral decrease of posterior alpha power (see de Vries, van Driel, Karacaoglu, & Olivers, 2018; Schneider, Barth, Haase, & Hickey, 2019). As these posterior alpha asymmetries were related to the spatial orienting of attention (Bae & Luck, 2018; Hakim, Adam, Gunseli, Awh, & Vogel, 2019), this effect should be independent of the number of cued vs. non-cued working memory representations. Furthermore, there should also be a non-retinotopic modulation of posterior alpha power following the retro-cues, as prior investigations revealed a stronger suppression when one compared to two mental representations were indicated as further-on task relevant (Poch, Valdivia, Capilla, Hinojosa, & Campo, 2018; Schneider et al., 2017). If such effects are evident following retro-cue and clearly prior to memory probe presentation, they might reflect higher demands on attentional control processes on the level of working memory (Fukuda, Mance, & Vogel, 2015; Fukuda, Woodman, & Vogel, 2015). Modulations in oscillatory alpha power by the number of cued or non-cued items shortly before or after memory probe onset, however, should rather be linked to a varying amount of working memory resources engaged for probe processing and the selective retrieval of relevant information.

Clarifying this sequence of retroactive attentional modulations in the current task will contribute to a better understanding of the cognitive mechanisms involved in retroactive attentional orienting. Furthermore, it is required to link the hypothesized EEG effects to the extent of proactive interference when responding to non-cued probes. Therefore, the described oscillatory parameters will be correlated with the RT difference between the non-

cued and new probe conditions on a between-subject level. This will clarify if and to what extent the described attentional mechanisms can be engaged to control for the interference of irrelevant information with ongoing working memory processes.

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 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 on which participants were instructed to constantly focus 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). Part of the items were presented on the vertical meridian, on either side of the fixation cross, and the rest were presented on the horizontal meridian. There were never more than two items on one dimension and the items were always presented at only one of the vertical and one of the horizontal positions (i.e., below vs. above and left vs. right of fixation). The items were aligned on a hypothetical circle with a 1.25° radius for the first position and 2.5° on the second position on each axis. When there was only one item on the vertical or horizontal meridian, 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, which were never task relevant

Afterwards, the fixation point remained and 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 the participants kept focusing fixation before retro-cue onset. The cues lasted for 200 ms and were an indication of the axis (horizontal or vertical) of the memory array to be tested on later. For memory arrays with set-size two, 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.

After the retro-cue, there was an 800 ms inter-stimulus-interval followed by the probe stimulus. The participant had to indicate by button press if the colored disc presented as probe had been presented on the memory-array axis indicated by the retro-cue. There were three types of probe stimuli: cued probes (50% of all trials) when the probe had been presented on the indicated position, non-cued or ‘recent negative’ probes (20% of all trials; condition nonexistent following the neutral cue) when the probe had been on the non-cued position and

new probes (30% of all trials) when the 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 break after the fourth block was five minutes long. The whole procedure took 2.5 to 3 hours, including preparation of the EEG setup.

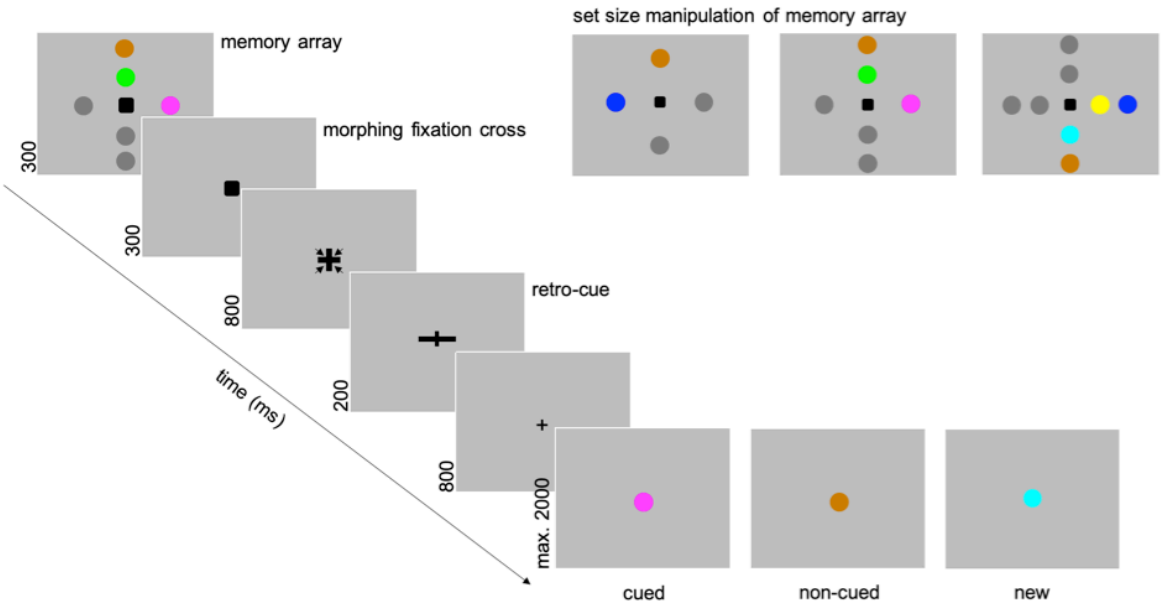

Figure 1. Experimental design. A memory array differing in set size from two to four relevant (colored) items was followed by a retro-cue indicating either all (neutral condition; only for set-size two) or only the lateral vs. central items as task-relevant. The later probe display either contained a 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 (i.e., 'positive' vs. 'negative' decisions). All responses prior to 150 ms after the onset of the memory probe were labeled as 'premature responses' and also treated as errors.

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 employed 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; Bell & Sejnowski, 1995) was run on every second epoch and ADJUST (Mognon, Jovicich, Bruzzone, & Buiatti, 2011) was used 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 also 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

In a first analysis step, we focused on changes in oscillatory power following retro-cue presentation irrespective of the position of the cued and non-cued items. In this regard, 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. Non-lateralized oscillatory power

The pre-stimulus interval served as spectral baseline for all analyses of non-lateralized oscillatory power. Certain electrodes of interest were defined for assessing the oscillatory responses following the memory array: A frontal midline electrode cluster surrounding FCz position (i.e., Fz, FC1, FCz, FC2, Cz) and a cluster including channels over left and right-hemispheric parieto-occipital and parietal cortex (PO7, PO3, P7, P5, PO8, PO4, P8, P6; see Schneider et al., 2019) were defined to measure both higher-level executive control function and the processing of working memory representations in posterior visual areas. Based on these channels, we combined the experimental conditions in four conditions based on the number of cued and non-cued items following the retro-cues. The conditions with a two-item and three-item memory array followed by a one-item retro-cue constituted the 'one-item cued' condition, while the conditions with a three-item and four-item memory and a two-item retro composed the 'two-items cued' condition. The condition with a two-item memory array and a one-item retro-cue and with a three-item memory and a two-item retro-cue constituted the 'one-item non-cued' condition. Accordingly, the condition with a three-item memory array and a one-item retro-cue and with a four-item memory and a two-item retro-cue constituted the 'two-items non-cued' condition. Differences in oscillatory power at the pre-defined electrode clusters were then assessed based on a cluster-permutation procedure:

Based on 1000 permutations, the conditions with one vs. two cued items were randomly assigned for each dataset and within-subject *t*-tests were run for each time-frequency data point. This resulted in a 52 (frequencies) x 200 (times) x 1000 (permutations) matrix. Subsequently, *p*-values within these matrices were searched for $p < 0.01$ and the maximum cluster meeting this condition was assessed for each permutation. Differences between conditions in the original data were considered for post-hoc testing when the size of *p*-value clusters based on $p < 0.01$ (see solid lines in figures 3 & 4) or $p < 0.05$ (see dashed lines in

figures 3 & 4) were larger than the 95th percentile of the permutation-based distribution of cluster sizes. The same procedure was run for conditions with one vs. two non-cued items.

Further statistical analyses of non-lateralized oscillatory power were based on repeated-measures ANOVAs with the factors *'cued items'* (one vs. two) and *'non-cued items* (one vs. two) and based on the time-frequency clusters featuring significant differences in the cluster-permutation procedures. The analyses of posterior oscillatory power included a further within-subject factor for *'hemisphere'* (left vs. right). In case post-hoc ANOVAs were based on a time-frequency cluster following memory probe presentation, they also included a within-subject factor for *'probe-type'* (cued vs. non-cued vs. new). This was done in order to investigate if and to what extent retroactive attentional processes related to the cued or non-cued items would bias the proactive interference effect.

While analyses up to here only included the selective retro-cue conditions, we also wanted to assess the mechanisms involved in working memory updating on a more general level. Therefore, the 'set-size two' condition with a one-item retro-cue was compared to the neutral condition (also memory array set-size two) based on separate within-subject *t*-tests for the time-frequency clusters resulting from the above-described cluster-permutation procedure.

2.5.2. 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 6A). 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 6B). 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 already 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 and additionally 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 comparison required correcting for cumulative Type 1 error (indicated as adjusted *p*-values or p_{adj} for *t*-test parameters).

2.5.3. 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). This was achieved by concentrating on both asymmetric oscillatory power relative to the position of the cued or non-cued mental representations and the non-retinotopic oscillatory response averaged across memory array stimulus positions. Non-retinotopic ERSPs with a pre-stimulus baseline were measured at left- and right-hemispheric posterior lateral channels (PO7, PO3, P7, P5 vs. PO8, PO4, P8, P6) and the fronto-central electrode cluster (Fz, FC1, FCz, FC2, Cz) and averaged across all experimental conditions except for those including a neutral retro-cue. The neutral conditions did not feature a non-cued memory probe and thus did not allow for calculating a proactive interference effect on behavioral level. Separately for the three

electrode clusters, each ERSP data point was then correlated with the RT difference between the non-cued and new probe conditions by means of a 'between-subject' Spearman rank correlation. Time frequency clusters featuring reliable correlations between oscillatory power and RT difference were assessed with a cluster-permutation approach: First, we randomly assigned measured ERSPs to RT differences on a between-subject level based on 1000 permutations. For each data point within each permutation, we calculated Spearman's rho and assessed how likely this correlation coefficient was relative to the permutation-based distribution of remaining correlation coefficients for this data point. Afterwards, resulting *p*-values for each time-frequency point were searched for clusters with $p < 0.1$ (hardly any clusters were evident in the permuted data with the $p < 0.01$ criterion used above) and the maximum cluster size was measured per permutation. This resulted in 1000 normally distributed cluster sizes. A time-frequency cluster in the original data was considered as statistically significant when its size based on *p*-values < 0.01 (indexing the statistical significance of the Spearman correlation) was larger than the 95th percentile of the permutation-based distribution of cluster sizes.

For hemispheric asymmetries, we calculated the contralateral minus ipsilateral ERSP differences at posterior lateral channels (PO7/8, PO3/4, P7/8, P5/6), averaged across all memory array set-size conditions except for the conditions including a neutral retro-cue. We then used the difference between the distractor lateral and target lateral conditions as a general marker for attentional selectivity and calculated between-subject correlations as described above (cf. supplementary figure S1).

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, $t(23)=-0.893$, $p=0.381$, $d_z=-0.182$.

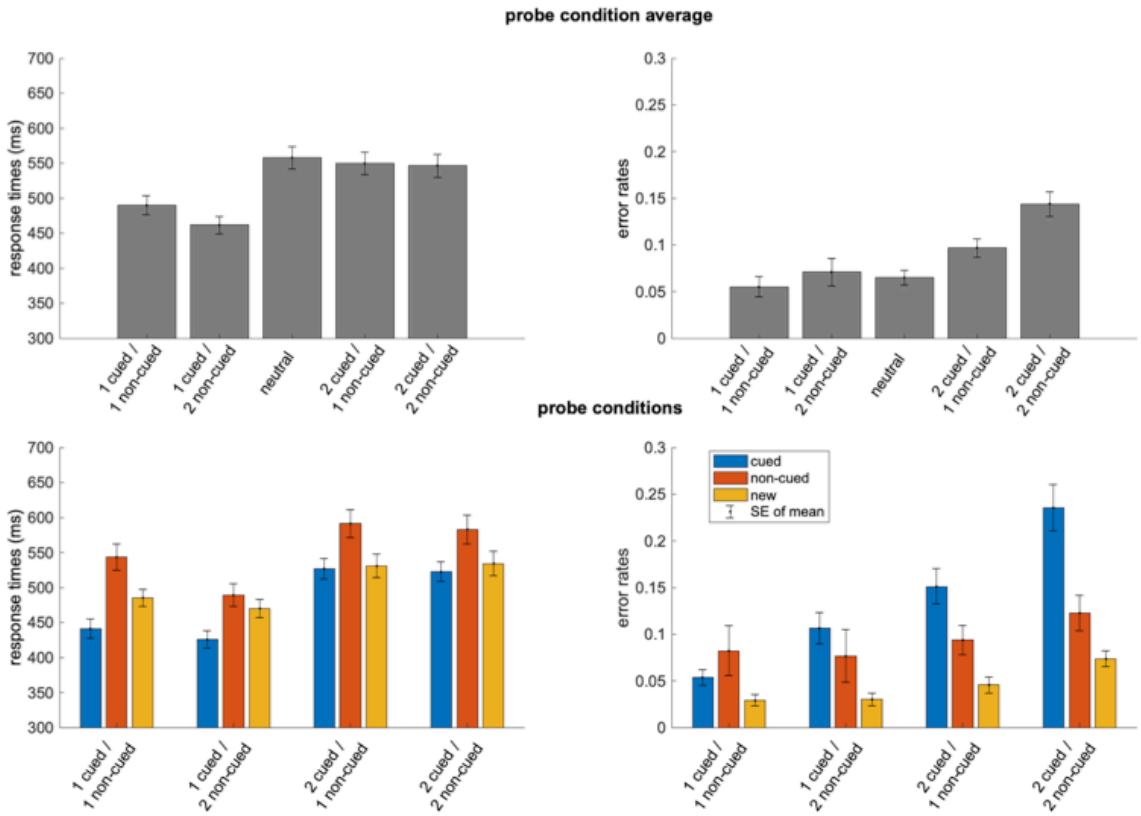

Figure 2. Behavioral results. The upper plots show the response times and error rates for the different retro-cue conditions, averaged across memory probe conditions. The lower plots depict response time and error rate patterns as a function of probe condition. The neutral condition was not displayed 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 a 'negative' 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. Additionally, RTs were also 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. Non-lateralized oscillatory power

For the posterior lateral electrode cluster, oscillatory power in theta frequency range showed an early modulation by the number of cued items following the memory array (see figure 3A). As this effect appeared prior to retro-cue presentation, it must have been related to differences in the sensory processing of the memory array as a function of the varying set-sizes in the experimental conditions compared (i.e., higher average set-size for the two-items cued condition). The same was true for the later effect in posterior alpha power with an increased suppression for the two-items cued condition. A similar effect was also evident when comparing posterior oscillatory power as a function of the number of non-cued items (with a higher average set-size for the two-items non-cued condition; see figure 3B). Post-hoc analyses centered on the time-frequency ranges (i.e., 650-1000 ms; 6-13 Hz) included within-subject factors for the number cued items, non-cued items and *hemisphere*. It was shown that the effect of the number of cued items was strongest over the right hemisphere, $F(1,23)=9.647$, $p=0.005$, $p_{crit}=0.05$, $\eta^2_p=0.296$. The same was true for the number of non-cued items, $F(1,23)=7.961$, $p=0.01$, $p_{crit}=0.029$, $\eta^2_p=0.257$ (see figure 3C). No further interactions based on these factors were evident (all p-values > 0.2).

Following the retro-cues, posterior oscillatory modulations by the number of cued vs. non-cued items were clearly different: For the number of cued items, a stronger suppression for the one-item cued conditions appeared in upper alpha and beta frequency ranges (10-25 Hz) prior to memory array onset (2200-2500 ms after memory array onset; see figure 3A). Post-hoc analyses indicated that this effect did not reveal any interaction with the factor *hemisphere* or the number of non-cued items (all p-values > 0.3). The comparison regarding the number of non-cued items further revealed a stronger suppression of alpha power when two items were indicated as irrelevant (7-12 Hz; 1900-2300 ms after memory array onset; see figure 3B). While the earlier effect related to memory array set-size appeared in the same

frequency range, this modulation did not differ as a function of *hemisphere*, $F(1,23)=1.776$, $p=0.196$, $p_{crit}=0.021$, $\eta^2_p=0.072$. Additionally, the frontal electrode cluster featured a comparable modulation by the number of non-cued items, as also evident in the effect topographies (see figures 3C & 4C).

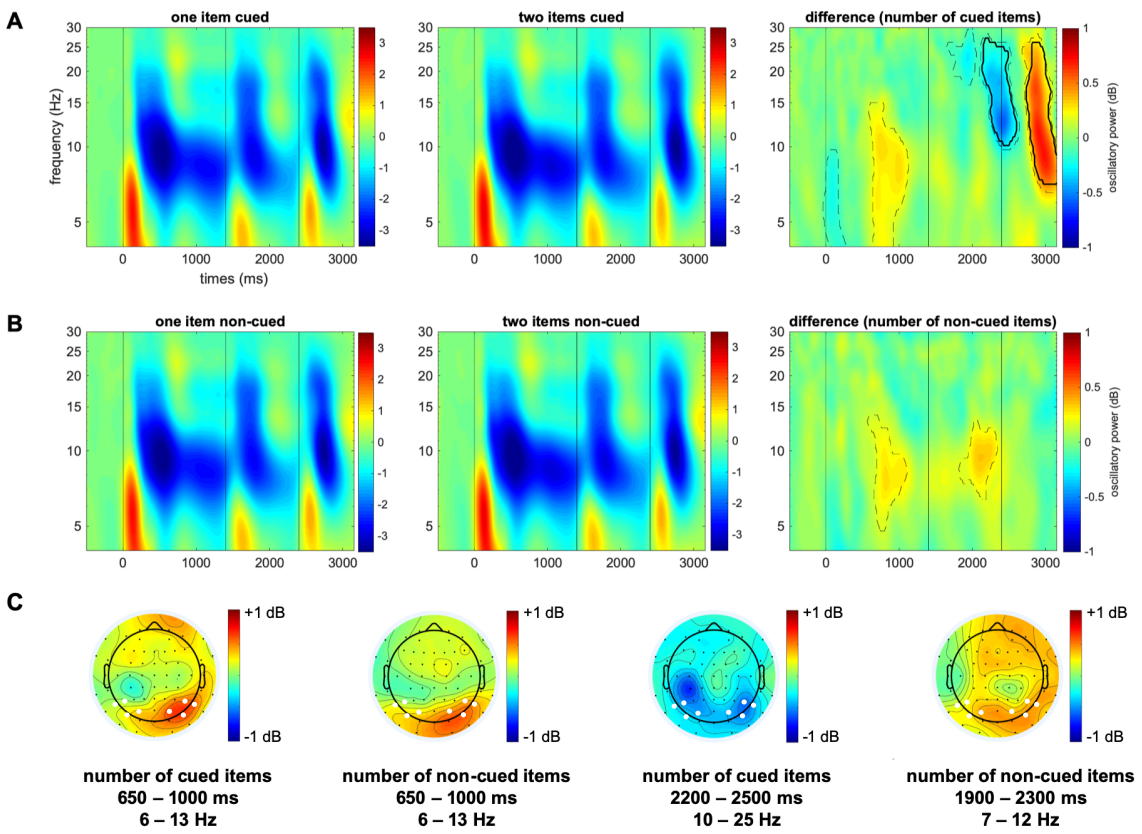

*Figure 3. Oscillatory power (dB) at posterior lateral channels. **A** depicts the retro-cue conditions averaged across 'one item' vs. 'two-items' retro-cues. The oscillatory response as a function of the number of non-cued items is shown in **B**. Results of cluster permutation statistics for p<0.01 (solid lines) and p<0.05 (dashed lines) are indicated in the difference plots (one minus two cued items; one minus two non-cued items). Vertical lines indicate the onsets of the memory array, retro-cue and memory probe. **C** shows the topographic effects of four relevant effect clusters. Analyzed electrode clusters are marked in white.*

The number of cued items also led to an effect from lower alpha to beta frequencies (7-25 Hz) around 600 ms following the memory probes, both at posterior and frontal sites (see figures 3A & 4A) and possibly related to response execution or evaluation processes. The cluster-permutation analyses performed on the frontal electrodes further revealed an increased suppression in beta frequency range (17-25 Hz; 1750-2450 ms after memory array onset) for the one-item cued condition prior to the onset of the memory probes. As evident in the

respective topography (see figure 4C), this was rather related to an effect with a maximum over left central and fronto-central sensors.

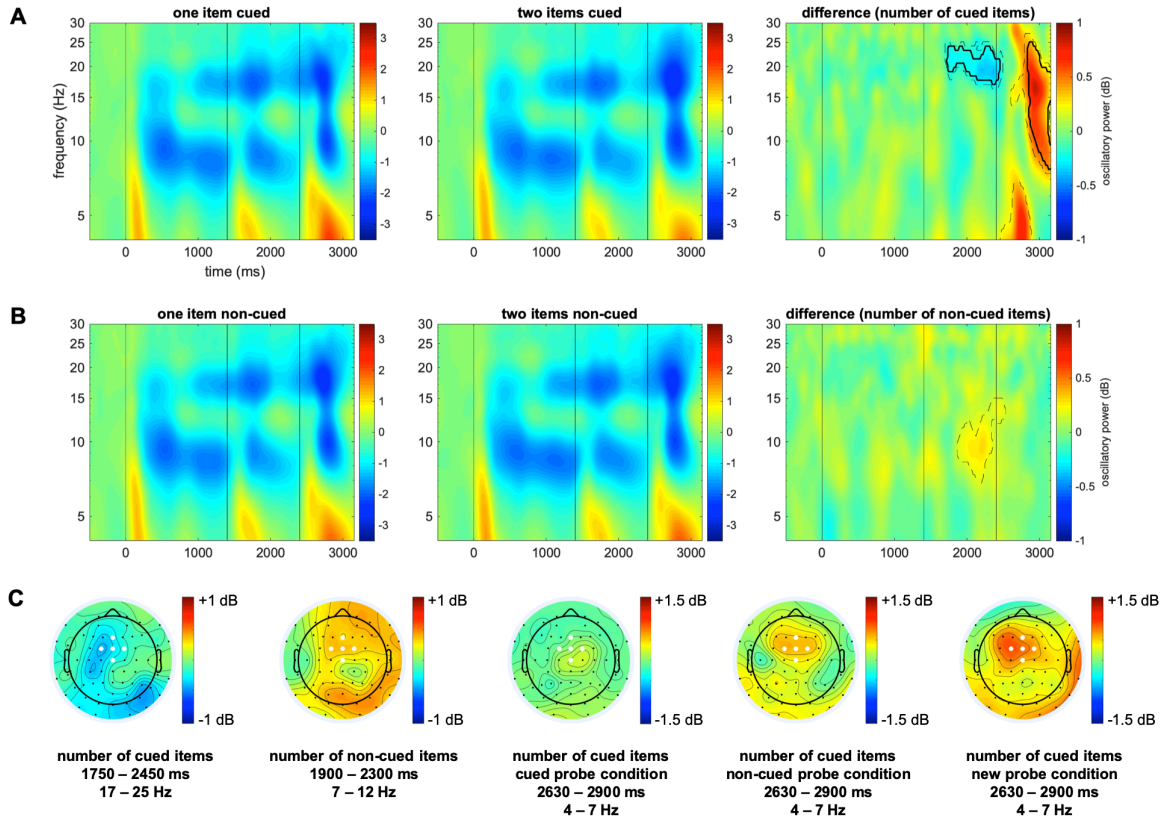

*Figure 4. Oscillatory power (dB) at frontal channels. **A** depicts the retro-cue conditions averaged across 'one item' vs. 'two-items' retro-cues. The oscillatory response as a function of the number of non-cued items is shown in **B**. Results of cluster permutation statistics for $p<0.01$ (solid lines) and $p<0.05$ (dashed lines) are indicated in the difference plots (one minus two cued items; one minus two non-cued items). Vertical lines indicate the onsets of the memory array, retro-cue and memory probe. **C** shows the topographic effects of three relevant effect clusters, with the effect of the number of cued items on frontal theta power displayed separately for each probe condition. Analyzed electrode clusters are marked in white.*

A further fronto-central effect of the number of cued items was evident in theta frequency range following the memory probe display, with a stronger oscillatory power for one compared to two cued items (see figure 4A). Post-hoc analyses centered on this time and frequency range (4-7 Hz; 2630-2900 ms after memory array onset) tested whether this effect of the number of cued items was further modulated by *probe-type*. There was a respective interaction, $F(1,23)=4.134$, $p=0.029$, $\varepsilon=0.843$, $p_{crit}=0.033$, $\eta^2_p=0.152$, and further analyses revealed that only the non-cued, $t(23)=4.484$, $p_{adj}<0.001$, $d_z=0.915$, and new probe conditions,

$t(23)=3.09$, $p_{adj}=0.008$, $d_z=0.631$, featured a stronger frontal theta response following one-item retro-cues (see topographies in figure 4C; cued probe: $t(23)=0.975$, $p_{adj}=0.34$, $d_z=0.199$).

We further compared the oscillatory responses between selective vs. neutral retro-cues within conditions with memory arrays composed of two items. The first theta response was increased following selective vs. neutral retro-cues. This effect appeared for both the frontal and posterior electrode clusters and was followed by a stronger suppression of posterior alpha power for the selective retro-cue condition (see figure 5). These modulations were followed by an increase in higher alpha and beta power (10-17 Hz) for the selective retro-cue condition prior to memory probe presentation (2100-2350 ms after memory array onset, 10-17 Hz; see figure 5). Also theta oscillatory power after memory probe presentation was increased in the selective retro-cue condition, but only for the frontal electrode cluster. As also observed for the analyses based on the number of cued vs. non-cued items, there was a modulation of the oscillatory response in alpha and beta frequency range (7-25 Hz) in an interval overlapping with the given responses. This effect is likely related to response execution or evaluation processes and is of no central interest for the current investigation.

3.3. Hemispheric asymmetries in oscillatory power

As illustrated in figure 6, cluster-corrected comparisons between the target lateral and distractor lateral conditions (averaged across all conditions with selective retro-cues) revealed a latency interval with reliable difference in alpha frequency range (8-13 Hz) from approximately 450 to 780 ms after retro-cue onset (see figure 6A). 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, $F(1,23)=2.877$, $p=0.103$, $\eta^2_p=0.111$, or non-cued items, $F(1,23)=0.307$, $p=0.585$, $\eta^2_p=0.013$. Also the three-way interaction was statistically non-significant, $F(1,23)=0.932$, $p=0.344$, $\eta^2_p=0.039$.

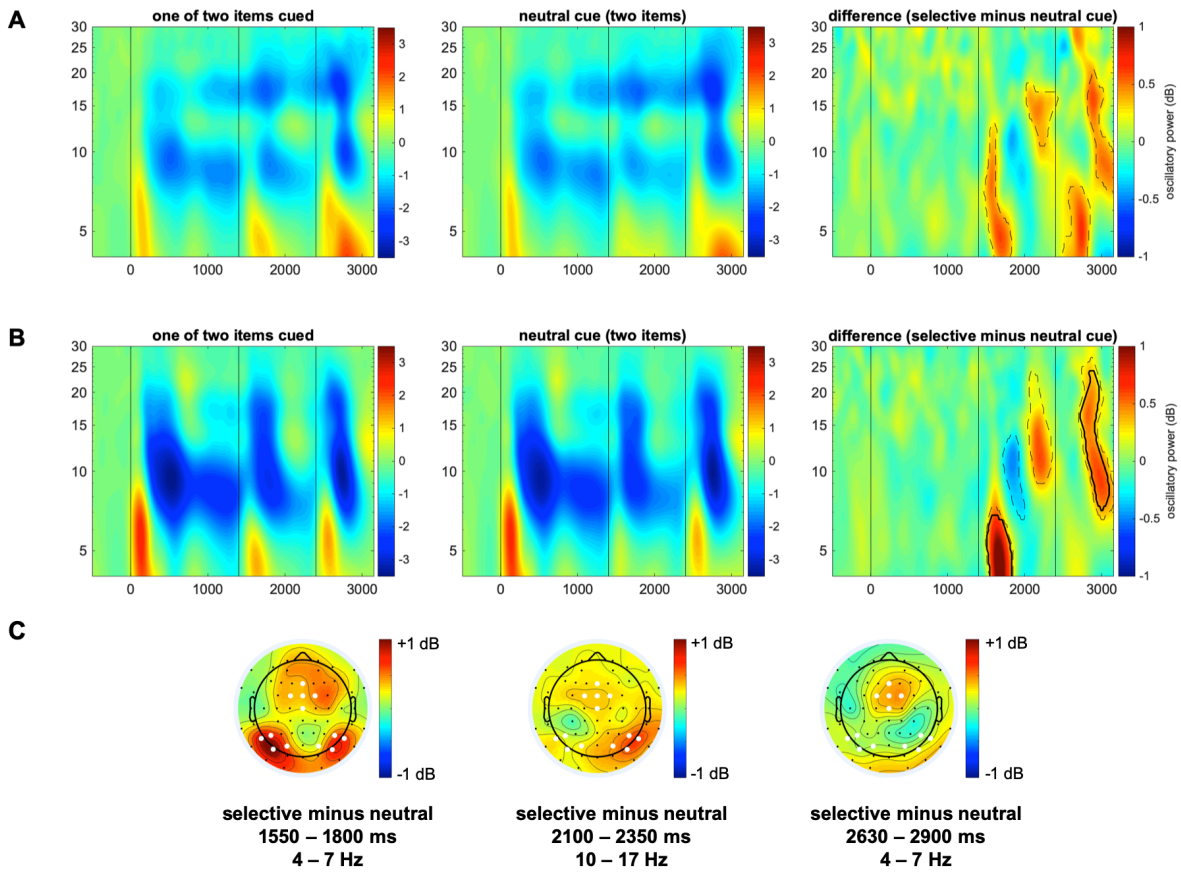

*Figure 5. Oscillatory power (dB) for selective vs. neutral retro-cue conditions. **A** depicts the time-frequency plots for the frontal electrode cluster. The oscillatory response for the posterior lateral electrode clusters is shown in **B**. Results of cluster permutation statistics for p<0.01 (solid lines) and p<0.05 (dashed lines) are indicated in the difference plots (selective minus neutral condition). Vertical lines indicate the onsets of the memory array, retro-cue and memory probe. **C** shows the topographic effects of three relevant effect clusters. Analyzed electrode clusters are marked in white.*

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 6B). This again brought up a time-frequency area with a statistically reliable difference between condition 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).

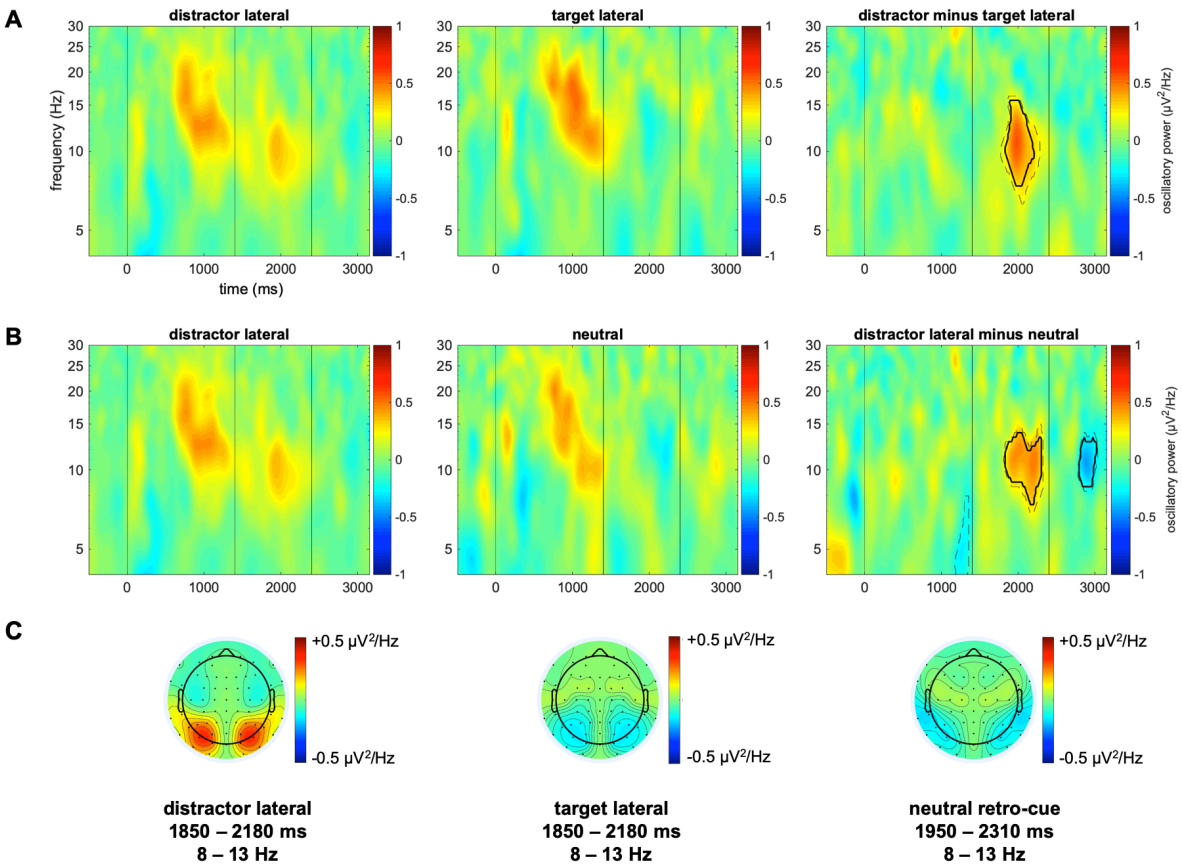

*Figure 6. Hemispheric asymmetries in oscillatory power. **A** depicts the comparison of the distractor lateral and target lateral contralateral-ipsilateral differences. The respective comparison of the distractor lateral and neutral conditions is shown in **B**. Vertical lines indicate the onsets of the memory array, retro-cue and memory probe. The topographies of these effects (**C**) are mirrored at the central electrode axis, because contralateral and ipsilateral signals are averaged across left- and right hemispheres.*

As clearly evident from prior analyses, the number of cued or non-cued items from the memory array did not influence differences in lateralized alpha power between target and distractor lateral conditions following the retro-cues. 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 (see Schneider et al., 2019; de Vries et al., 2018), 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.

3.4. Correlational analyses

These analyses were run in order to relate the effects on the level of oscillatory power 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. While no reliable EEG-behavior correlations were observed on the level of posterior hemispheric asymmetries in oscillatory power (see supplementary figure S1), the extent of alpha/beta suppression around memory probe presentation (~2200-2500 ms after memory array onset; 10-21 Hz) reliably predicted the non-cued minus new probe difference on RT level. This correlation was most clearly evident over right-hemispheric posterior electrodes (see figure 7A). A minor correlation was also evident over left-hemispheric posterior electrodes, but was reduced to the interval following memory probe presentation (see figure 7B).

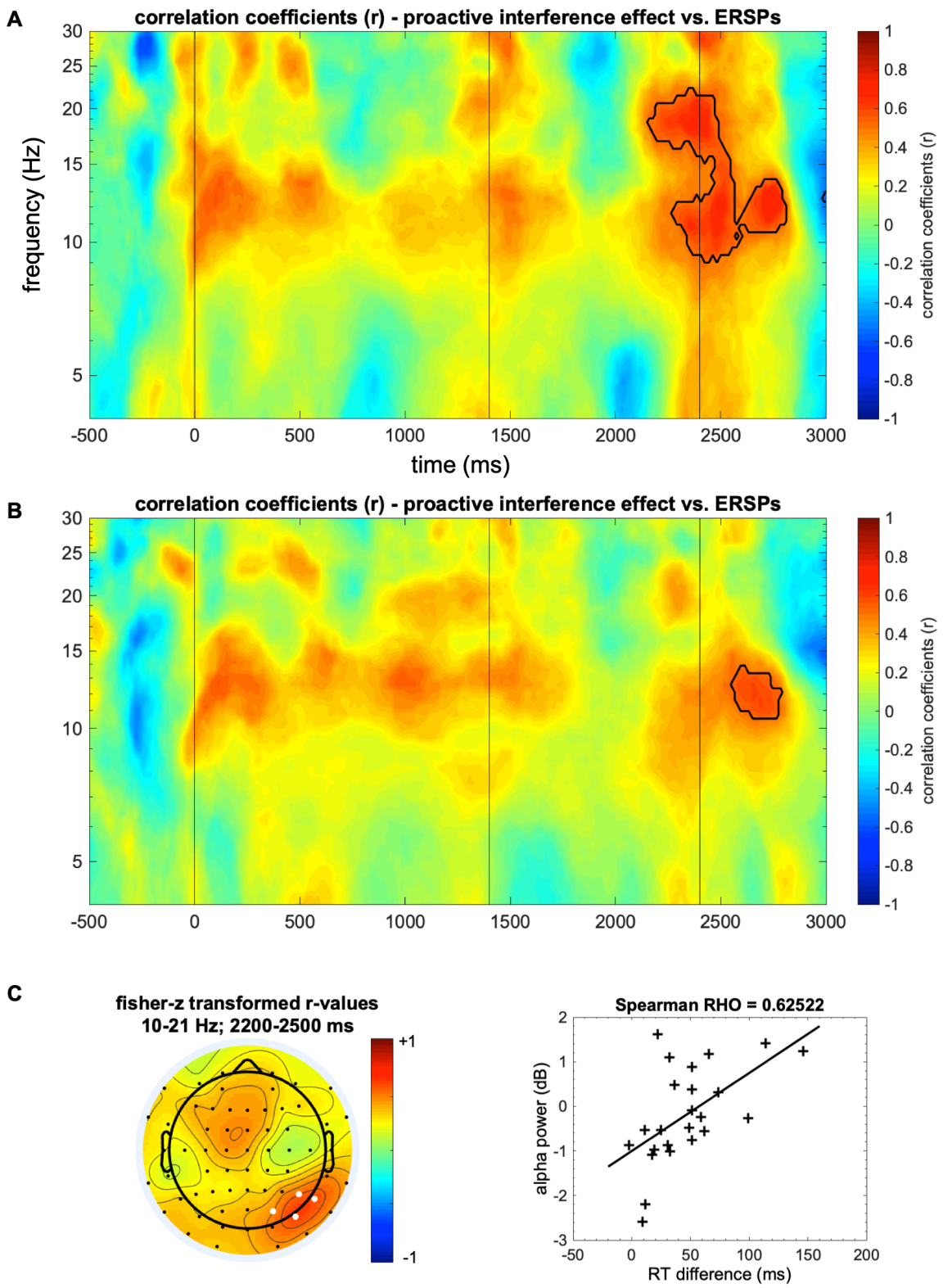

*Figure 7 Between-subject correlations for right (**A**) and left posterior lateral electrode clusters (**B**). The plots show the correlations coefficients for each time-frequency point. Vertical lines indicate the onsets of the memory array, retro-cue and memory probe. The lower plots (**C**) depict a topography of fisher-z transformed correlation coefficients centered on the significant cluster for right-sided channels and the respective correlation plot within the same time-frequency range.*

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, Sussman, & Jiang, 2008b; Schneider 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 et al., 2015; Schneider et al., 2015). These findings might be related to a special representational status of a single item within the focus of attention in working memory (Myers, Stokes, & Nobre, 2017; Schneider et al., 2017). Participants already know about the probed working memory content following the retro-cues. This obviates a working memory retrieval process during probe processing and allows for storing the cued information in a response-related representational state (Schneider et al., 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[1] following the retro-cues that might in turn be applied during probe processing.

4.1. Frontal theta power signals general demands on cognitive control

The nature of this result pattern on behavioral level can further be approached by considering the oscillatory EEG correlates of retroactive attentional orienting and cognitive control mechanisms within the current experimental setting. The focus in these analyses was based on finding oscillatory correlates of cognitive processes composing the ability to deal with irrelevant working memory contents.

Increases in frontal theta power were related to the signaling of the need for attentional control mechanisms (Arnau, Wascher, & Küper, 2019; Cavanagh & Frank, 2014; Sauseng, Griesmayr, Freunberger, & Klimesch, 2010) . Referred to the current task, retroactively cuing the relevant items demanded an attentional control process and thus led to an increase in frontal and posterior theta power and a subsequent decrease in posterior alpha power relative to the neutral cue condition (see figure 5). However, theta oscillations in response to the retro-cues were not modulated by the number of cued or non-cued items (see figure 4). This indicates that increased theta power reflected the general demands on attentional control for working memory updating following the retro-cues and not the inhibitory control of non-cued mental representations or a cognitive control process in preparation for proactive interference during later working memory retrieval. During memory probe processing, we furthermore observed a more specific effect in the frontal midline theta response (see figure 4). Theta

[1] The current experimental was not designed for differentiating if retroactive attentional selection leads to a release of mental resources previously occupied by the storage of non-cued representations or of those engaged in attentional control over working memory contents. ‘Working memory resources’ and ‘attentional resources’ will thus be used interchangeably.

power was increased when only one item was retroactively cued, but this effect was limited to memory probes demanding a 'negative decision' (memory probes with non-cued and new colors). This indicates that with only one attended working memory item, a higher extent of cognitive control was reactively applied in support of the formation of a 'negative decision'. Thus, the frontal theta response following both the retro-cues and probe stimuli was not specifically related to the compensation of proactive interference, but to the more general engagement of higher-level control mechanisms on the level of working memory. This is in line with earlier findings showing that increases in frontal low-frequency power can consistently be found in working memory tasks that require differing types of higher-level control processes (de Vries et al., 2018; Johnson et al., 2017; Sauseng et al., 2010).

4.3. Hemispheric alpha power asymmetries reflect excitatory and inhibitory subprocesses for spatial attentional focusing

While characteristics of frontal theta oscillations reflect higher-level attentional control mechanisms, the processing of the stored information itself is associated with modulations of posterior alpha power (Bae & Luck, 2018; Hakim et al., 2019; Myers et al., 2015; Poch et al., 2014; Schneider et al., 2015, 2016). Here, we assessed both alpha power effects independent from stimulus position (see figures 3-5) and retinotopic modulations of posterior alpha power by focusing on posterior hemispheric asymmetries (see figure 6). As hypothesized, the retinotopic modulations of posterior alpha power, depicted by hemispheric asymmetries following retro-cue presentation, were insensitive to the number of cued or non-cued working memory items. While this was already indicated by an earlier investigation (see Poch et al., 2018), we further corroborated the notion that retroactive attentional orienting is based on both excitatory and inhibitory attentional sub-processes (de Vries et al., 2018; Schneider et al., 2019): As indicated in figure 6, hemispheric asymmetries in alpha power differed between conditions with lateral targets and lateral distractors or non-cued mental representations.

While there was a stronger contralateral suppression of posterior alpha power when a lateral item was cued, alpha power was increased contralateral to the positions of non-cued working memory content (relative to the ipsilateral content that was defined as task-irrelevant already with memory array presentation). Thus, the orienting of the focus of attention in working memory was based on both an excitatory process related to target position and an inhibitory process related to withdrawing attention from the non-cued position (Schneider et al., 2019). Importantly, also the neutral retro-cue condition featured a contralateral suppression of alpha power relative to the position of the lateral memory array item. This indicates that the alpha asymmetries following the retro-cues were indeed based on the retinotopic positions of memory array items and depicted the attentional processing of only the laterally presented information.

The fact that the number of cued or non-cued items did not further modulate these hemispheric asymmetries indicates that they were related to spatial attentional processes for internally drawing the focus of attention to the position of the cued items and not to the selective remembering or forgetting of cued vs. non-cued non-spatial information content (Bae & Luck, 2018; Hakim et al., 2019). In line with this notion, we did not find a relationship between the extent of the hemispheric asymmetries and the manifestation of the proactive interference effect (see supplementary figure S1). Of course, this lack of a significant EEG-behavior correlation might be related to a problem of statistical power with between-subject correlational analyses based on only 24 datasets. Yet, it might also indicate that while an inhibitory process is required to spatially detach the focus of attention from irrelevant working memory representations, this process does not likewise suppress the irrelevant non-spatial information content.

4.2. Posterior alpha power as a correlate of engaged working memory resources

We further found that, independent from stimulus position, there was a stronger suppression of posterior alpha and beta power when only one item was retroactively cued[2] (see figure 3). This effect was previously shown in retroactive cuing studies by Poch and colleagues (Poch et al., 2018) and our lab (Schneider et al., 2017). Importantly, the respective modulation appeared closely linked in time to the onset of the memory probe and around 800 ms after retro-cue presentation. This time frame renders it unlikely that the effect was directly linked to retroactive attentional processes triggered by the cues. Such attentional modulations should appear around 400 – 500 ms after retro-cue presentation, in the same time frame as the hemispheric asymmetries in alpha power (see above). Even more importantly, alpha power suppression cannot be linked to a reduction of the number of representations activated in working memory following the retro-cues. Prior investigations suggested that a representation in working memory is coded by means of low-frequency oscillations in neuronal clusters and is individuated from other representations by means of phase differences (Raffone & Wolters, 2001; Siegel, Warden, & Miller, 2009). The oscillatory power measured at the scalp thus decreases with higher numbers of items activated in working memory. This implies that releasing certain items from active storage would be related to a relative increase in oscillatory power over posterior recording sites. We thus propose that the suppression of alpha/beta power was associated with the attentional resources engaged in preparation for the

[2] This effect was accompanied by a stronger suppression of alpha power over the left sensorimotor cortex (i.e., contralateral to the side of response) that can be linked to a response-related representational state when the working memory item to be probed was already determined by the retro-cue (see Schneider et al., 2017). However, this effect is not within the main focus of the current investigation.

processing of the memory probe display. Cuing one item allowed for the selective retrieval of the to-be-tested working memory content already prior to the memory probes, thereby facilitating the focusing of attention on probe processing and decision making (see Souza & Oberauer, 2016). Further support for this assumption comes from the comparisons of oscillatory power between the selective and neutral retro-cues. A neutral retro-cue had no demands on working memory updating and related attentional control functions, thus potentially allowing for a more efficient preparation for probe processing (as reflected in stronger alpha and beta power suppression in the neutral retro-cue condition shortly prior to probe presentation).

This interpretation of results is in line with earlier investigations showing that focusing attention on only one item in visual working memory leads to a freeing of resources for the attentional control of irrelevant sensory distractors in a working memory task (here reflected by a modulation of a posterior negative slow wave; see Barth & Schneider, 2018; Schneider et al., 2017; Schneider, Bonmassar, & Hickey, 2018). Additionally, a prior investigation on the temporal characteristics of the proactive interference effect in a retroactive cuing working memory task indicated that when delay intervals between the retro-cue and memory probes provided more time for updating working memory and preparing for probe onset, this led to a decline of the proactive interference effect (Schneider et al., 2016). This might either have been related to changes in the representational state of the non-cued information following the retro-cues or to a better focusing of attention on probe processing.

The functional meaning of alpha/beta power suppression prior to memory probe onset can be further conceived when also considering that this effect was positively related to the proactive interference effect on RT level. Participants with a small proactive interference effect showed lower oscillatory power in alpha/beta frequencies prior to memory probe onset (averaged across experimental conditions). This effect appeared in nearly the same time-frequency range as the within-subject modulation by the number of cued items. As posterior

alpha decreases with increasing demands in visual working memory tasks (Fukuda et al., 2015a; Fukuda et al., 2015b), this might in the same way imply that participants with lower posterior alpha power engaged more resources in anticipation of probe presentation. They could thus more efficiently retrieve the relevant information from working memory, thereby compensating for interference by irrelevant memory representations during decision making.

Regarding the number of non-cued working memory representations, alpha power was decreased over lateral posterior cortex and fronto-central sites for two items relative to one item. Importantly, this alpha power modulation was not a mere confound of the extent of resources applied on working memory storage. The set-size dependent alpha power modulation following the memory array was only evident over right posterior cortex and thus featured a topography distinct from the topography of the alpha power modulations following the retro-cues (see figure 5). Additionally, this effect cannot be related to varying inhibitory demands following the retro-cues, because an inhibitory process would be reflected by a relative increase in alpha power for conditions with a higher number of non-cued items (Sauseng et al., 2009). The stronger alpha power suppression might thus be related to a more efficient release of working memory resources with more items indicated as task-irrelevant or to increased demands when focusing attention within a relatively higher average number of working memory representations.

4.4. Conclusion

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. Non-lateralized effects in the oscillatory response to

the retro-cues and memory probes revealed that posterior alpha power was suppressed around memory probe presentation when only one compared to two items were retroactively cued (see figure 3). Furthermore, alpha power in this time-frequency range (averaged across experimental conditions) was positively correlated to the extent of proactive interference on RT level (see figure 7). This promotes the notion that focusing attention on only one item in working memory allows for a more efficient attentional preparation for memory probe processing, thereby decreasing the impact of irrelevant memory contents. A stronger suppression of oscillatory power, limited to alpha frequency range, was also shown with higher numbers of non-cued items following the retro-cues (see figure 3). In combination, these result patterns suggest that the reduced proactive interference effect in the '1 cued/2 non-cued' condition was related to the extent of attentional or working memory resources released prior to memory probe presentation.

Frontal theta was associated with the general demands on attentional control mechanisms in working memory (see also: de Vries et al., 2018; Sauseng et al., 2010). Theta power following the retro-cues was increased for the selective vs. neutral condition, but not as a function of the number of cued or non-cued items (see figure 5). Additionally, higher frontal theta power following the memory probes reflected the increase of top-down control in support of the formation of a 'negative' response when attention was previously focused on only one working memory item (see figure 4).

Hemispheric asymmetries in posterior alpha power following the retro-cues were insensitive to 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). Importantly, we showed that withdrawing the focus of attention from lateral working memory content caused a contralateral alpha power increase. On the contrary, retroactively shifting the focus of attention to lateral positions was related to a contralateral suppression of posterior alpha power (see figure 6). Shifting the spatial focus of attention within working

memory representations thus makes use of both excitatory and inhibitory attentional sub-processes to guarantee efficient target resolution.

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. https://doi.org/10.1162/jocn_a_01233

Arnau, S., Wascher, E., & Küper, K. (2019). Age-related differences in reallocating cognitive resources when dealing with interruptions. *NeuroImage*, *191*, 292–302. https://doi.org/10.1016/j.neuroimage.2019.02.048

Atkinson, R. C., & Juola, J. F. (1974). Search and decision processes in recognition memory. In *Contemporary developments in mathematical psychology: I. Learning, memory and thinking*. Oxford: W.H. Freeman.

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

Baddeley, A. (1996). Exploring the Central Executive. *Quarterly Journal of Experimental Psychology Section A: Human Experimental Psychology*, *49*(1), 5–28. https://doi.org/10.1080/713755608

Baddeley, A. D., & Hitch, G. J. (1974). Working Memory. In *The psychology of learning and motivation: Advances in research and theory* (pp. 47–89).

Bae, G.-Y., & Luck, S. J. (2018). Dissociable Decoding of Spatial Attention and Working Memory from EEG Oscillations and Sustained Potentials. *The Journal of Neuroscience*, *38*(2), 409–422. https://doi.org/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*, *55*(7), 1–15. https://doi.org/10.1111/psyp.13062

Beck, V., Luck, S. J., & Hollingworth, A. (2018). Whatever you do, don't look at the . . .: Evaluating guidance by an exclusionary attentional template. *Ournal of Experimental Psychology: Human Perception and Performance*, *44*(4), 645–662. https://doi.org/10.1037/xhp0000485

Bell, A. J., & Sejnowski, T. J. (1995). An information-maximisation approach to blind separation and blind deconvolution. *Neuronal Computation*, *7*(6), 1129–1159.

Cavanagh, J. F., & Frank, M. J. (2014). Frontal theta as a mechanism for cognitive control. *Trends in Cognitive Sciences*, *18*(8), 414–421. https://doi.org/10.1016/j.tics.2014.04.012

Cowan, Nelson. (1999). *An embedded-processes model of working memory*. https://doi.org/10.1017/CBO9781139174909.006

Cramer, A. O. J., van Ravenzwaaij, D., Matzke, D., Steingroever, H., Wetzels, R., Grasman, R. P. P. P., … Wagenmakers, E.-J. (2016). Hidden multiplicity in exploratory multiway ANOVA: Prevalence and remedies. *Psychonomic Bulletin & Review*, *23*(2), 640–647. https://doi.org/10.3758/s13423-015-0913-5

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. *Cerebral Cortex*, *28*(11), 4090–4104. https://doi.org/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. *Journal of Neuroscience Methods*, *134*(1), 9–21. https://doi.org/10.1016/j.jneumeth.2003.10.009

Desimone, R & Duncan, J. (1995). Neural Mechanisms of Selective Visual Attention. *Annual Review of Neuroscience*, *18*(1), 193–222. https://doi.org/10.1146/annurev.neuro.18.1.193

Failing, M., Wang, B., & Theeuwes, J. (2019). Spatial suppression due to statistical regularities is driven by distractor suppression not by target activation. *Attention, Perception, & Psychophysics*. https://doi.org/10.3758/s13414-019-01704-9

Fuchs, M., Kastner, J., Wagner, M., Hawes, S., & Ebersole, J. S. (2002). A standardized boundary element method volume conductor model. *Clinical Neurophysiology*, *113*(5), 702–712. https://doi.org/10.1016/S1388-2457(02)00030-5

Fukuda, K., Mance, I., & Vogel, E. K. (2015). Power Modulation and Event-Related Slow Wave Provide Dissociable Correlates of Visual Working Memory. *Journal of Neuroscience*, *35*(41), 14009–14016. https://doi.org/10.1523/JNEUROSCI.5003-14.2015

Fukuda, K, Woodman, G. F., & Vogel, E. K. (2015). Individual differences in visual working memory capacity: contributions of attentional control to storage. In *Mechanisms of sensory working memory: attention and performance XXV* (pp. 105–119). San Diego: Academic.

Gaspelin, N., Gaspar, J. M., & Luck, S. J. (2019). Oculomotor inhibition of salient distractors: Voluntary inhibition cannot override selection history. *Visual Cognition*, 1–20. https://doi.org/10.1080/13506285.2019.1600090

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

Gaspelin, N., & Luck, S. J. (2019). Inhibition as a potential resolution to the attentional capture debate. *Current Opinion in Psychology*, *29*, 12–18. https://doi.org/10.1016/j.copsyc.2018.10.013

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

Griffin, I. C., & Nobre, A. C. (2003). Orienting Attention to Locations in Internal Representations. *Journal of Cognitive Neuroscience*, *15*(8), 1176–1194. https://doi.org/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. *Psychological Science*, 15. https://doi.org/1o0i.1or1g7/170/.01197576/70957671997861390838043

Hickey, C., Di Lollo, V., & McDonald, J. J. (2009). Electrophysiological indices of target and distractor processing in visual search. *Journal of Cognitive Neuroscience*, *21*(4), 760–775. https://doi.org/10.1162/jocn.2009.21039

Hickey, C., McDonald, J. J., & Theeuwes, J. (2006). Electrophysiological Evidence of the Capture of Visual Attention. *Journal of Cognitive Neuroscience*, *18*(4), 604–613. https://doi.org/10.1162/jocn.2006.18.4.604

Johnson, E. L., Dewar, C. D., Solbakk, A.-K., Endestad, T., Meling, T. R., & Knight, R. T. (2017). Bidirectional Frontoparietal Oscillatory Systems Support Working Memory. *Current Biology*, *27*(12), 1829-1835.e4. https://doi.org/10.1016/j.cub.2017.05.046

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. *Journal of Neurophysiology*, *77*(1), 24–42. https://doi.org/10.1152/jn.1997.77.1.24

Makovski, T., Sussman, R., & Jiang, Y. V. (2008a). Orienting attention in visual working memory reduces interference from memory probes. *Journal of Experimental*

Psychology: Learning, Memory, and Cognition, *34*(2), 369–380. https://doi.org/10.1037/0278-7393.34.2.369

Makovski, T., Sussman, R., & Jiang, Y. V. (2008b). Orienting attention in visual working memory reduces interference from memory probes. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *34*(2), 369–380. https://doi.org/10.1037/0278-7393.34.2.369

Mognon, A., Jovicich, J., Bruzzone, L., & Buiatti, M. (2011). ADJUST: An automatic EEG artifact detector based on the joint use of spatial and temporal features: Automatic spatio-temporal EEG artifact detection. *Psychophysiology*, *48*(2), 229–240. https://doi.org/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. *Attention, Perception, & Psychophysics*, *74*(8), 1590–1605. https://doi.org/10.3758/s13414-012-0358-0

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

Myers, N. E., Stokes, M. G., & Nobre, A. C. (2017). Prioritizing Information during Working Memory: Beyond Sustained Internal Attention. *Trends in Cognitive Sciences*, *21*(6), 449–461. https://doi.org/10.1016/j.tics.2017.03.010

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. *Journal of Cognitive Neuroscience*, *27*(3), 492–508. https://doi.org/10.1162/jocn_a_00727

Nobre, A. C., Griffin, I.C., & Rao, A. (2008). Spatial attention can bias search in visual short-term memory. *Frontiers in Human Neuroscience*, *1*. https://doi.org/10.3389/neuro.09.004.2007

Pertzov, Y., Bays, P. M., Joseph, S., & Husain, M. (2013). Rapid forgetting prevented by retrospective attention cues. *Journal of Experimental Psychology: Human Perception and Performance*, *39*(5), 1224–1231. https://doi.org/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. *European Journal of Neuroscience*, *40*(2), 2399–2405. https://doi.org/10.1111/ejn.12589

Poch, C., Valdivia, M., Capilla, A., Hinojosa, J. A., & Campo, P. (2018). Suppression of no-longer relevant information in Working Memory: An alpha-power related mechanism?

Biological Psychology, *135*, 112–116. https://doi.org/10.1016/j.biopsycho.2018.03.009

Raffone, A., & Wolters, G. (2001). A Cortical Mechanism for Binding in Visual Working Memory. *Journal of Cognitive Neuroscience*, *13*(6), 766–785. https://doi.org/10.1162/08989290152541430

Rihs, T. A., Michel, C. M., & Thut, G. (2007). Mechanisms of selective inhibition in visual spatial attention are indexed by ?-band EEG synchronization. *European Journal of Neuroscience*, *25*(2), 603–610. https://doi.org/10.1111/j.1460-9568.2007.05278.x

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. https://doi.org/10.1126/science.aah7011

Sauseng, P, Griesmayr, B., Freunberger, R., & Klimesch, W. (2010). Control mechanisms in working memory: A possible function of EEG theta oscillations. *Neuroscience & Biobehavioral Reviews*, *34*(7), 1015–1022. https://doi.org/10.1016/j.neubiorev.2009.12.006

Sauseng, P, Klimesch, W., Heise, K. F., Gruber, W. R., Holz, E., Karim, A. A., … Hummel, F. C. (2009). Brain Oscillatory Substrates of Visual Short-Term Memory Capacity. *Current Biology*, *19*(21), 1846–1852. https://doi.org/10.1016/j.cub.2009.08.062

Sauseng, P, Klimesch, W., Stadler, W., Schabus, M., Doppelmayr, M., Hanslmayr, S., … Birbaumer, N. (2005). A shift of visual spatial attention is selectively associated with human EEG alpha activity. *European Journal of Neuroscience*, *22*(11), 2917–2926. https://doi.org/10.1111/j.1460-9568.2005.04482.x

Sawaki, R., & Luck, S. J. (2010). Capture versus suppression of attention by salient singletons: Electrophysiological evidence for an automatic attend-to-me signal. *Attention, Perception, & Psychophysics*, *72*(6), 1455–1470. https://doi.org/10.3758/APP.72.6.1455

Schneider, D., Barth, A., Haase, H., & Hickey, C. (2019). Hemispheric asymmetries in EEG alpha oscillations indicate active inhibition during attentional orienting within working memory Keywords. *Behavioural Brain Research*, *359*(July 2018), 38–46. https://doi.org/S0166432818309811

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. https://doi.org/10.1016/j.neuroimage.2017.08.057

Schneider, D., Bonmassar, C., & Hickey, C. (2018). Motivation and short-term memory in visual search: Attention's accelerator revisited. *Cortex*, *102*, 45–56. https://doi.org/10.1016/j.cortex.2017.06.022

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. *Behavioural Brain Research*, *293*, 114–124. https://doi.org/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. *Scientific Reports*, *6*(1), 21442. https://doi.org/10.1038/srep21442

Siegel, M., Warden, M. R., & Miller, E. K. (2009). Phase-dependent neuronal coding of objects in short-term memory. *Proceedings of the National Academy of Sciences*, *106*(50), 21341–21346. https://doi.org/10.1073/pnas.0908193106

Sligte, I. G., Scholte, H. S., & Lamme, V. A. F. (2008). Are there multiple visual short-term memory stores? *PLoS ONE*, *3*(2), 2–10. https://doi.org/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. *Journal of Neuroscience*, *30*(11), 4024–4032. https://doi.org/10.1523/JNEUROSCI.5684-09.2010

Souza, A. S., & Oberauer, K. (2016). In search of the focus of attention in working memory: 13 years of the retro-cue effect. *Attention, Perception, & Psychophysics*, *78*(7), 1839–1860. https://doi.org/10.3758/s13414-016-1108-5

Souza, A. S., Rerko, L., & Oberauer, K. (2014). Unloading and reloading working memory: Attending to one item frees capacity. *Journal of Experimental Psychology: Human Perception and Performance*, *40*(3), 1237–1256. https://doi.org/10.1037/a0036331

Stokes, M. G. (2015). 'Activity-silent' working memory in prefrontal cortex: A dynamic coding framework. *Trends in Cognitive Sciences*, *19*(7), 394–405. https://doi.org/10.1016/j.tics.2015.05.004

Theeuwes, J. (2018). Visual Selection: Usually Fast and Automatic; Seldom Slow and Volitional. *Journal of Cognition*, *1*(1). https://doi.org/10.5334/joc.13

Vandenbroucke, A. R. E., Sligte, I. G., & Lamme, V. A. F. (2011). Manipulations of attention dissociate fragile visual short-term memory from visual working memory.

Neuropsychologia, *49*(6), 1559–1568. https://doi.org/10.1016/j.neuropsychologia.2010.12.044

Whitney, P., Arnett, P. A., Driver, A., & Budd, D. (2001). Measuring Central Executive Functioning: What's in a Reading Span? *Brain and Cognition*, *45*(1), 1–14. https://doi.org/10.1006/brcg.2000.1243

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

Wolff, M. J., Jochim, J., Akyürek, E. G., & Stokes, M. G. (2017). Dynamic hidden states underlying working-memory-guided behavior. *Nature Neuroscience*, *20*(6), 864–871. https://doi.org/10.1038/nn.4546

Woodman, G. F., & Luck, S. J. (2003). Serial Deployment of Attention During Visual Search. *Journal of Experimental Psychology: Human Perception and Performance*, *29*(1), 121–138. https://doi.org/10.1037/0096-1523.29.1.121

Worden, M. S., Foxe, J. J., Wang, N., & Simpson, G. V. (2000). *Anticipatory Biasing of Visuospatial Attention Indexed by Retinotopically Specific ⎵-Band Electroencephalography Increases over Occipital Cortex*. *20*(6), RC63–RC63.