Research report

Hemispheric asymmetries in EEG alpha oscillations indicate active inhibition during attentional orienting within working memory

Daniel Schneiderb,⁎, Anna Göddertz, Henrike Haase, Clayton Hickeyb,1, Edmund Waschera,1

a Leibniz Research Centre for Working Environment and Human Factors, TU, Dortmund, Germany
b School of Psychology, University of Birmingham, UK

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A B S T R A C T

Working memory contents can be prioritized by retroactively deploying attention within memory. This is broadly interpreted as evidence of a concentration of memory resources to the attended, to-be-remembered stimulus. However, online attentional selection is known to additionally depend on distractor inhibition, raising the viable alternative that attentional deployment in working memory involves inhibitory control processes. Here, we demonstrate that active inhibition plays a central role in the deployment of attention in working memory. We do so using a retroactive cueing paradigm, where a briefly presented memory array is followed by a cue indicating a to-be-remembered target (Experiment 1) or a to-be-forgotten distractor (Experiment 2). We identify discrete indices of target selection and distractor inhibition in lateralized oscillatory activity over visual areas. When a retroactive cue identifies the location of a target, results show rapid decrease of lateral, target-elicited alpha band activity, representing attentional orienting toward the target. This is followed only later by emergence of an increase in distractor-elicited alpha activity, reflecting distractor inhibition. In contrast, when the retroactive cue identifies a distractor, evidence of distractor inhibition emerges first, only later followed by target selection. These results thus demonstrate that separate excitatory and inhibitory processes underlie the deployment of attention on the level of working memory representations.

1. Introduction

Our environment provides us with a dynamic stream of visual input. Objects often appear fleetingly, disappearing before we are able to deploy the cognitive resources that support detailed analysis and categorization. We are able, however, to store this rich stream of information for several seconds in high-volume, medium-duration visual memory. By deploying attention within this representation, we can resolve information about visual objects even when the objects themselves are no longer present in the environment. Information that is relevant for ongoing or future behavior can thus be activated in working memory [1–3]. However, it is unclear exactly how attentional selection within this memory system is instantiated.

The online deployment of attention to stimuli physically present in the environment is thought to be antagonistic in nature: stimuli ‘compete’ for access to limited-capacity resources located downstream from perception like those involved in decision-making and behavioral control. Attention resolves this competition by enhancing representations of attended stimuli and by inhibiting representations of unattended stimuli [4,5]. Attentional suppression has been conceptualized as a product of the volitional, top-down deployment of attention [6], and as an automatic lateral inhibition between target templates and distractor representations [4]. But it is not obvious that attention within memory relies on comparable sub-processes. Representations in working memory lying outside the focus of attention appear intrinsically fragile and of limited duration [7,8]. They are easily overwritten by new visual inputs [9,10] and possibly decay by default [11]. In this context, attentional selection may not involve the inhibition of working memory representations, but rather act solely as a preservative that saves attended stimuli from otherwise-pervasive decay and interference.

Here we investigate if and how distractor inhibition is involved in attentional orienting within visual working memory. We do so using a paradigm in which cues indicate the task relevance of a visual object after that object has disappeared from the display. These kind of retroactive cues (retro-cues) provide roughly the same benefit to memory performance as do cues that precede stimulus onset [12,13] and they have similar correlates in hemispheric asymmetries of alpha oscillatory power in EEG [14–17]. Increases in alpha power have been linked to...
the proactive suppression of distractors, for example in results showing that alpha power increases over sensory areas representing upcoming irrelevant input [18–21]. However, alpha asymmetry has not been clearly linked to inhibition regarding the orienting of attention within working memory. This is due to the fact that prior studies were typically based on relative alpha power differences between cortical areas representing either relevant or irrelevant content (for review [22]).

In order to test the possibility that inhibitory control is required to drop distractor stimuli from the focus of attention in working memory, we isolated EEG indices of target and distractor processing in a working memory task. This was achieved by manipulating the memory array such that task-relevant stimuli were presented at central and lateral locations before one object was subsequently identified as a to-be-remembered (Experiment 1) or to-be-forgotten (Experiment 2) item. This manipulation of laterality allows for the unambiguous association of hemispheric asymmetries to lateral stimuli, because central stimuli evoke equivalent activity in both visual hemispheres [23,24].

If distractor suppression is involved in the deployment of attention in working memory, our expectation was to observe an increase in alpha power contralateral to the location of the task-irrelevant stimulus. To foreshadow, this pattern emerges in our results. To further determine whether this reflects an active inhibitory process, in a subsequent experiment we explicitly instructed participants to forget the cued stimulus. Our expectation was that if the contralateral increase in alpha power reflects an inhibitory mechanism independent from the selection of working memory contents, this explicit ‘forget’ instruction should accentuate the effect.

2. Materials and methods

2.1. Participants

Twenty participants (9 females; M(age) = 25.15 years, SD = 3.58 years, range: 19–30 years) took part in Experiment 1 and an independent group of 16 participants took part in Experiment 2 (7 females; M(age) = 25.06 years, SD = 3.33 years, range: 19–29 years). All participants were right-handed, none reported any known neurological or psychiatric disease, and all had normal vision (without correction). Participants were reimbursed for their time with either cash (10 € per hour) or course credit. 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

Stimuli were generated on a computer equipped with a ViSaGe MKII Stimulus Generator (Cambridge Research Systems, Rochester, UK) and displayed on a 22-inch CRT monitor (100 Hz; 1024 × 768 pixels) at a viewing distance of 150 cm. Throughout the whole trial, a black fixation cross was presented on a dark gray background (luminance of 15 cd/m²). Participants were instructed to maintain fixation throughout the course of each trial and this was monitored via an SMI Red 500 eye-tracker (120 Hz; SensoMotoric Instruments, Teltow, Germany). Fixation was defined as maintenance of eye position within 1° of the fixation cross. The eye-tracker was calibrated at the beginning of each experimental block and each trial began only when participants maintained fixation for at least 40 ms in a 100 ms interval. Trials were not aborted when fixation was broken during the trials. In both experiments, the inter-trial interval varied randomly in steps of 1 ms from 500 to 1000 ms (rectangular distribution). It was extended by an average of 409 ms (SD = 198.72 ms) by the fixation control procedure. Each experiment was comprised of 960 trials divided into 8 blocks of trials, each separated by a 2-min break.

2.2.1. Experiment 1

The memory array was composed of three bars (0.1 by 1° of visual angle; see Fig. 1) presented with random orientation, under the constraint that orientation had to differ between the bars by at least 15°.
The bars were aligned on a hypothetical circle with 1.5° radius and presented at 60° (right), 180° (bottom) and 300° (left). Thus, one bar was presented below fixation on the vertical meridian and the other two bars presented to the left and right slightly above the horizontal meridian. One of the lateralized bars was gray (25 cd/m²) while the two remaining bars were red (CIE: 0.566, 0.376, 0.25; 25 cd/m²) and blue (CIE: 0.168, 0.131, 0.25; 25 cd/m²). The gray bar was never task relevant, and the two colored bars never appeared contralateral to one another. The gray bar was displayed in order to make sure that both visual hemispheres were equally activated during sensory processing of the memory array. The memory array was presented for 200 ms and followed 800 ms later by the appearance of either a retro-cue (50% of trials; retro-cue condition) or a memory probe (50% of trials; early probe condition).

In the retro-cue condition, the fixation cross increased in size and acquired either red or blue color, identifying the task-relevant stimulus from the now-absent memory array. In 2/3 of retro-cue trials, the cued item had appeared at a lateral location (target lateral condition). In the remaining trials, the cued item had appeared on the vertical meridian of the display, such that the other colored item appeared at a lateral location (distractor lateral condition). In this condition, hemispheric EEG asymmetries could not be associated with the selection of the lateral gray item, because it was defined as task-irrelevant. This allowed for unambiguous measurement of the hemispheric asymmetry related to the non-cued colored stimulus at the lateral position.

When a central bottom item was cued, both left- and right-hemispheric visual areas were equally involved in its further processing. The disengagement of attention from the non-cued item, however, should express predominantly in the contralateral hemisphere. On the contrary, when a lateral item was cued, its selection should express primarily in the contralateral hemisphere, whereas inhibitory processes related to the irrelevant item should express equally in both hemispheres.

The retro-cue appeared for 100 ms and was followed 900 ms later by the response probe. The response probe was a randomly oriented black bar (0 cd/m²) presented at fixation. Participants were asked to match the orientation of this bar to the orientation of the cued memory item by moving the computer mouse, which changed the orientation of the probe, and pressing the left mouse button when they felt the orientation of the probe matched the orientation of the remembered item. They had 3 s. to make this response (see Fig. 1).

In the early probe condition, the retro-cue was replaced by a memory probe presented in the color of the relevant memory array stimulus that sustained for 3 s. Because early probes and retro-cues were presented at the same latency in the trial, working memory retrieval began at the same time in both conditions. This ensured that conditional differences could not result from variance in the time-based decay of working memory representations [25]. The proportion of the target vs. distractor lateralized conditions was equal in the retro-cue and early probe conditions.

2.2.2. Experiment 2

Experiment 2 was designed to determine if attentional suppression indexed in Experiment 1 was a product of automatized lateral inhibition in visual cortex, or rather an active, volitional inhibitory process. In contrast to Experiment 1, the early probe condition was omitted from Experiment 2, and the meaning of the retro-cue changed halfway through the experiment. In the ‘remember cue’ condition, the cue had the same meaning as in Experiment 1 and identified the target in the now-absent memory array. In the novel ‘forget cue’ condition, the cue identified the colored non-target item. The order of these conditions was counterbalanced across participants.

2.3. Behavioral analyses

Angular error was calculated by subtracting the orientation that participants reported via manipulation of the memory probe from the orientation of the cued item in the memory array. As we considered only the absolute value in this regard, angular errors ranged from 0 to 90°. The standard deviation (SD) of the angular error within each experimental condition was considered as a further parameter for assessment of working memory accuracy. These values were adjusted for circularity using the CircStat Toolbox for MATLAB® [26]. We additionally measured both the onset of the computer mouse movement and the time of the button press that indicated response confirmation. While response confirmation should vary as a function of the difference in orientation between the cued item and the memory probe, the onset of computer mouse movement provides a reliable measure of the time required for response preparation. Participants confirmed their response within the time limit in 99.81% of trials (SD = 0.29%) in Experiment 1 and 99.32% of trials (SD = 0.97%) in Experiment 2. Only these trials were retained for behavioral analysis.

We also fitted a mixture model to orientation matching performance. This segmented the response distribution into four parameters [27]. Kappa (κ) reflects the precision of the recalled working memory representation independent from the item identified for recall. Parameters pT, pN, pU and pU refer to the probability of reporting orientation of the target item (pT), the probability of reporting orientation of the non-target (pN), and the probability of reporting at random (pU).

2.4. EEG recording and preprocessing

EEG was recorded at 1000 Hz. from 64 Ag/AgCl passive electrodes (EasyCap GmbH, Herrsching, Germany) in extended 10/20 scalp configuration using a NeurOne Tesla AC-amplifier (Bittium Biosignals Ltd, Kuopio, Finland). A 250 Hz low-pass filter was used during recording, AFz was employed as ground electrode, and FCz was employed as reference. Impedance was kept below 10kΩ for all electrodes.

Analysis was conducted using MATLAB® and the EEGLAB toolbox [28]. 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 before the data were re-referenced to the average of all channels. Channels with kurtosis exceeding 5 SD (Experiment 1: M = 6 channels, SD = 1.6; Experiment 2: M = 6 channels, SD = 0.97) were replaced with a spherical spline interpolation of immediately proximal channels. Anterior lateral channels (F9, F10, AF7, AF8, AF3, AF4, Fp1, Fp2) were not considered for rejection and interpolation, as this would have impaired reliable identification of eye movements within our data. Data epochs were created beginning 1000 ms before and ending 3000 ms after presentation of the memory array. Infomax independent component analysis (ICA [29]) was run on every second epoch and ADJUST [30] was used to detect and remove components related to eye blinks, vertical eye-movements and generic data discontinuities. Additionally, we computed single dipoles for each IC by means of a boundary element head model [31], and excluded components with a dipole solution with more than 40% residual variance. This procedure was followed by an automatic trial rejection 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 165 trials on average (SD = 51.97) in Experiment 1 and 177 trials on average in Experiment 2 (SD = 51.46). In an additional step, we excluded trials containing EEG correlates of lateral eye-movements. This was done by selecting the lateral frontal channels F9/F10 and then sliding a 200 ms time window in steps of 10 ms within an interval from 200 ms before to 1000 ms after presentation of the retro-cues (Exp. 1 and Exp. 2) or early probes (Exp. 1). 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 200 ms windows at F9 or F10 was greater than 20 μV [32]. This led to an additional rejection of 0–56 trials (M = 11.45, SD = 16.53) in Experiment 1 and 0–68 trials (M = 15.63, SD = 19.54) in Experiment 2. Residual influence of lateral eye movements was then corrected by excluding the
respectively ICS by visual inspection. The pre-processing steps for ERP analyses differed slightly from those prior to time-frequency analyses and are described in more detail in the supplement to this manuscript.

2.5. Time-frequency analyses

Event-related spectral perturbation (ERSP [28]) was computed by convolving three-cycle complex Morlet wavelets with each epoch of the EEG data. These analyses were based on 200 time points from −1000 to 3000 ms, centered on the appearance of the memory array, and frequencies ranging from 4 to 30 Hz were extracted in 52 logarithmic steps. The number of cycles instantiated in the wavelets increased from 3 cycles at 4 Hz to 11.25 cycles for 30 Hz. Baseline normalization was based on the time window prior to the presentation of the memory array. Following prior research on hemispheric alpha asymmetries in the context of attentional orienting [33–37], results from both experiments reflect the aggregated signal at posterior lateral electrode sites PO7/8, PO3/4, P7/8 and P5/6. Only trials where participants made a response confirmation to the probe were included in these analyses.

2.6. Statistical analyses

2.6.1. Experiment 1

Behavioral parameters were contrasted across the retro-cue and the early probe conditions by means of within-subject t-tests (two-sided). Effect size is indicated via Cohen’s $d$ for dependent measures.

Time-frequency analyses began with calculation of the ERSP signal at electrode locations contralateral and ipsilateral to targets and distractors separately in data collapsed across the retro-cue and early probe conditions. The contralateral minus ipsilateral differences were statistically contrasted between the distractor lateral and target lateral conditions by means of within-subject t-tests for each ERSP data point with subsequent application of FDR correction for multiple comparisons [38]. We then identified further conditional differences with an ANOVA including within-subject factors for asymmetry (contralateral vs. ipsilateral), eliciting stimulus (distractor lateral vs. target lateral) and cue-type (retro-cue vs. early probe).

2.6.2. Experiment 2

Within-subject t-tests (two-sided) were applied to compare behavioral performance between the ‘remember cue’ and ‘forget cue’ conditions. Cohen’s $d$, for dependent measures is used as an indicator for effect size.

Regarding the time-frequency analyses, we also began by identifying a latency and frequency window of interest. To this end, we averaged across the remember and forget cue conditions and then calculated the contralateral vs. ipsilateral portions of the ERSPs. Attentional modulations in the ERSPs were measured by statistically contrasting FDR-corrected contralateral minus ipsilateral differences between the target lateral and distractor lateral conditions.

We additionally tested if ‘remember cues’ and ‘forget cues’ had discernible impact on the latency of retroactive attentional orienting reflected in hemispheric alpha asymmetries. Latencies were measured based on the contralateral and ipsilateral ERSPs in an interval from 200 to 1000 ms following the retro-cues. In line with earlier research, the latency of the alpha asymmetry was defined as the time point when the areas under the contralateral-minus-ipsilateral difference curves (positive values for distractor lateral condition; negative values for target lateral condition) reached 50% of their total value [39,40].

An ANOVA with amplitudes of hemispheric alpha asymmetries as dependent variables included within-subject factors for asymmetry (contralateral vs. ipsilateral), eliciting stimulus (distractor lateral vs. target lateral) and cue-type (remember vs. forget cue). The latencies of alpha power asymmetries were used as dependent variables in an ANOVA including within-subject factors for eliciting stimulus and cue-type. In both Experiment 1 and 2, post-hoc comparisons were based on the Tukey’s Honest Significant Difference procedure. Partial eta squared ($\eta^2_p$) is reported as an indicator for effect size.

3. Results

3.1. Behavioral data

3.1.1. Experiment 1

No difference in angular error or variance in error was observed.
between the retro-cue (angular error: M = 10.347, SD = 1.956; standard deviation: M = 13.375, SD = 2.626) and the early probe conditions (angular error: M = 10.389, SD = 2.361; standard deviation: M = 13.663, SD = 3.386), t(19) = −0.233, p = 0.819, d = −0.052, and t(19) = −0.911, p = 0.374, d = −0.204, respectively. This indicates that the retro-cues did not lead to an increase in overall accuracy (see Fig. 2A). However, both response confirmation (retro-cue: M = 1122 ms, SD = 170 ms; early probe: M = 1285 ms, SD = 154 ms), t(19) = −9.977, p < 0.001, d = −2.231, and movement onset (retro-cue: M = 265 ms, SD = 71 ms; early probe: M = 475 ms, SD = 57 ms), t(19) = −12.48, p < 0.001, d = −2.791, occurred more quickly in the retro-cue condition (see figures 2B & 2C).

There was a trend toward lower probability of random reports (pU) in the retro-cue condition (M = 0.013, SD = 0.020) compared to the early probe condition (M = 0.021, SD = 0.024), t(19) = −1.726, p = 0.101, d = −0.386. No other trends emerged from this analysis, pY: t(19) = 1.571, p = 0.133, d = 0.351 (retro-cue: M = 0.982, SD = 0.022; early probe: M = 0.975, SD = 0.027), all other p-values > 0.56. Overall, these findings point toward a behavioral benefit of the retro-cue that manifested in speed of response but not response accuracy.

3.1.2. Experiment 2

The angular error reliably differed between the remember (M = 10.673, SD = 2.031) and forget cue conditions (M = 11.456, SD = 2.807), t(15) = −2.355, p = 0.033, d = −0.539, as did error variance (remember cue: M = 14.005, SD = 2.965; forget cue: M = 15.085, SD = 3.635), t(15) = −2.1, p = 0.053, d = −0.525. Accuracy thus slightly improved following a remember cue (Fig. 2D).

Mouse movement onset also occurred earlier in the remember cue condition (M = 227 ms, SD = 85 ms) compared to the forget cue condition (M = 262 ms, SD = 89 ms) (Fig. 2F), t(15) = −2.655, p = 0.018, d = −0.664, with no effect emerging in the latency of response confirmation (remember cue: M = 1239 ms, SD = 257 ms; forget cue: M = 1263 ms, SD = 186 ms) (Fig. 2E), t(15) = −0.574, p = 0.575, d = −0.143. No effects were identified in mixture model analysis (all p-values > 0.13).

3.2. Time-frequency data

3.2.1. Experiment 1

As illustrated in Fig. 3, FDR-corrected comparisons between the target lateral and distractor lateral conditions revealed a latency interval with reliable lateral difference in the alpha frequency range (10–12 Hz) from approximately 430 ms to 600 ms after the onset of the retro-cue or probe display. Subsequent analysis was focused on this time and frequency interval. There was a main effect of cue-type, F(1,19) = 32.418, p < 0.001, ηp² = 0.63, indicating a stronger alpha power suppression over posterior sites for the early probe compared to the retro-cue condition. The main effects of eliciting stimulus, F < 1, and asymmetry, F(1,19) = 2.073, p = 0.166, ηp² = 0.098, were not significant. However, as also indicated in the FDR-corrected t-tests, there was a reliable eliciting stimulus by asymmetry interaction, F(1,19) = 38.831, p < 0.001, ηp² = 0.671. This interaction was based on a contralateral vs. ipsilateral increase in alpha power for the distractor lateral condition (MD = 0.292 dB, SE = 0.08 dB, p = 0.002) and the absence of a reliable asymmetry effect in the target lateral condition (MD = −0.085 dB, SE = 0.076 dB, p = 0.272) (Fig. 3). The retro-cue and the early probe conditions did not differ regarding this interaction of asymmetry and eliciting stimulus, F < 1 (see Fig. 4). Overall, these results indicate that the lateralization of posterior alpha power as a marker of retroactive attentional orienting is closely related to the handling of the non-cued information.

3.2.2. Experiment 2

We further investigated if the posterior alpha asymmetries following retro-cues differed as a function of whether these cues indicated the need to forget or remember the stimulus. As shown in Fig. 5, FDR-corrected comparisons between the target lateral and distractor lateral conditions revealed a significant difference from 8 to 10 Hz and at about 600 ms to 730 ms following the retro-cue. Only the eliciting stimulus by asymmetry interaction reached significance in the subsequent ANOVA, F(1,15) = 27.702, p < 0.001, ηp² = 0.649, all other Fs < 1. Whereas the distractor lateral condition led to a contralateral vs. ipsilateral increase in posterior alpha power (MD = 0.275 dB, SE = 0.094 dB, p = 0.002), alpha power was decreased contralateral to a lateral target (MD = −0.343 dB, SE = 0.095 dB, p = 0.003). Target enhancement and distractor inhibition processes in working memory did thus not differ between the remember and forget cues based on the amplitudes of hemispheric alpha power asymmetries (see topographies in Fig. 5).

For the latency measures, the ANOVA identified a reliable eliciting stimulus by cue-type interaction, F(1,15) = 8.184, p = 0.012, ηp² = 0.353, all other Fs < 1. The alpha asymmetry emerged earlier for forget cues when the distractor was lateral (MD = −121 ms, SE = 64.944 ms, p = 0.082), but emerged earlier for remember cues when the target was lateral (MD = 76.25 ms, SE = 43.355 ms, p = 0.099) (Fig. 6). This suggests that remember cues sped target selection whereas forget cues sped distractor inhibition. As a side note, this interaction was also observed when considering the time point of 20% total area under the curve as a marker for the onset of the posterior alpha asymmetries, F(1,15) = 8.294, p = 0.011, ηp² = 0.356, but not when the time point of 80% area under the curve was used, F(1,15) = 1.281, p = 0.276, ηp² = 0.079, indicative of an effect on the early phases of retroactive attentional orienting.

In addition to the analyses of hemispheric alpha power asymmetries, we further calculated contralateral vs. ipsilateral patterns in ERPs over frontal channels for assessing lateral eye-movements and over posterior channels for investigating correlates of the active storage of information in working memory (i.e., contralateral delay activity; CDA [41]). These analyses are provided as a supplement to this manuscript.

4. Discussion

This study investigated the role of inhibition in the orienting of attention within working memory. In our general paradigm, a memory array was presented briefly to participants before a subsequent retro-cue identified either a target (Experiment 1) or distractor (Experiment 2) in that display. The target and distractor were present in each trial and could appear at central or lateral positions in the array.

Behavioral results in Experiment 1 indicated that participants were faster to report characteristics of a cued target relative to a control condition (see Fig. 2A–C). This was observed both in the speed with which they began to make their response and in the speed with which they ultimately confirmed their response, suggesting that retro-cues led to faster completion of both response preparation and execution. This is in line with the idea that retro-cues can create a head-start in memory retrieval and response planning [42–44]: in the retro-cue condition the representation of the cued stimulus could be selected and used to guide response preparation before the appearance of the probe, whereas in the control condition these processes could only occur in the same time frame. A further explanation for the retro-cue benefit on the speed of response might be a focusing of working memory storage on the cued item ahead of the memory probes. However, as described in more detail within the Supplementary material to this manuscript (see Supplementary figure S1B), we did not observe the CDA effect that would be predicted by this hypothesis. The cue had no benefit to accuracy in our results relative to the control condition, possibly due to the fact that participants reached ceiling performance. In studies with higher set-sizes of the memory arrays, the retro-cue can provide a robust accuracy benefit [45,46].

To investigate whether attentional deployment within working
memory involved the inhibition of the non-cued stimuli, or whether it was exclusively related to the selection of relevant memory contents, we looked to hemispheric asymmetries in alpha power. Several studies have identified hemispheric alpha power asymmetries as a correlate of retroactive attentional orienting, e.g. [14–17, 47, 48]. Poch, Capilla and colleagues [47] for example, presented endogenous color retro-cues that identified memory items presented on the left or right side of fixation and revealed a greater decrease in alpha power contralateral to the cued stimuli. This effect did not sustain throughout the delay period and was thus associated with a temporary attentional process rather than working memory storage.

Existing studies have discussed the possibility that inhibitory
mechanisms contribute to attentional deployment in working memory [22,49,50]. For example, based on a change detection paradigm and cues presented prior to the first stimulus array, Sauseng and colleagues [21] showed that ipsilateral alpha synchronization increased with the number of irrelevant stimuli that had to be suppressed. But the majority of investigations on attentional deployment during working memory storage have favored the notion that alpha asymmetries are related solely to selective target processing [14,17,50,51]. In support of this...
Supplementary data section provides results from single-trial correla-
tion analyses clearly showing that posterior alpha power asymmetries were
unrelated showing that posterior alpha power asymmetries were unrelated to EEG correlates of lateral eye movements. To further sup-
port these findings, future studies should additionally allow for tem-
porally aligning the EEG signal to eye tracking data. The present ex-
perimental setup was not suited for such analyses.

The current results raise a question regarding the possibility that
eccitatory and inhibitory attentional processes indexed in lateral alpha
power might qualify as markers for modulations in the representational
states of the individual working memory contents. As it stands, we
cannot confirm this idea. We showed that both excitatory and in-
hibitory processes are involved in shifting the focus of attention within
working memory. Inhibitory control appears required to detach the
focus of attention from the non-cued item and to support target selec-
tion. However, this does not necessarily imply that selected mental
representations were strengthened or that non-cued representations
were weakened following the retro-cues.

In fact, there are several recent demonstrations that dissociate the
selective deployment of spatial attention (as measured by hemispheric asymmetries in alpha power) and the manipulation of working memory
representations [51,53]. For example, non-lateralized posterior alpha
power has been found to desynchronize with an increasing number of
retro-cued items (see also [43]), whereas hemispheric alpha asymme-
tries seem insensitive to this manipulation [50]. Alpha power asym-
metries might thus not reflect mechanisms for enhancement or inhibi-
tion on the level of the individual mental representations, but be more
closely tied to the locus of selective attention.

In the current experiments, targets were cued with 100% validity.
This allowed for confident withdrawal of attention from the non-cued
object, and confident selection of the target, making it likely that target
information was available to subsequent cognitive operations [13].
Results have shown that this selection process does in fact lead to im-
proved high-level target representation [45]. Once such a higher-level
mental representation has been established, it may be no longer neces-
sary to keep a visuo-spatial representation of the cued object re-
presentation in working memory. Consistent with this idea, we did not
observe a CDA effect following the retro-cues, even when items at lat-
eral positions were cued as task-relevant (see Supplementary figure
S1B).

Our results, which demonstrate a role for active inhibition in at-
tentional deployment within working memory, are generally in line
with the notion that inhibitory control plays a broad role in memory
across a range of cognitive domains. Existing results have shown that
proactive inhibition prevents irrelevant external stimuli from con-
suming working memory capacity, e.g. [18]. Furthermore, inhibition
plays an important role in the reduction of interference when retrieving
information from long-term memory. In this case, inhibitory control
mechanisms initiate forgetting of memory traces competing with the
retrieval of relevant contents (i.e., retrieval induced forgetting [54]).
Interestingly, Waldhauer, Johansson and Hanslmayr demonstrated
that the forgetting of competing memories during long-term memory
retrieval is reflected in hemispheric alpha asymmetries [55], compar-
able to proactive and retroactive attentional orienting on working
memory level. This comparability in EEG signatures across cognitive
domains might indicate a general underlying process, perhaps in-
stated at the level of working memory that is probed here.

4.1. Conclusion

In summary, we report an increase in lateral posterior alpha power
as a correlate of active inhibition in visual working memory. Hemispheric alpha asymmetries observed in response to retro-cues in
earlier studies [14–17,47,48] thus appear related to both the selection
of the relevant mental representations and to an inhibitory control
process that enables the ability to shift attention away from irrelevant
information sources. Our results further demonstrate that cues identi-
fying stimuli that needed to be forgotten speed distractor inhibition, as
indexed in lateral alpha, whereas cues identifying stimuli that needed to be remembered speed attentional selection, again as indexed in lateral alpha. This suggests that target selection and distractor inhibition are separable active processes involved in the retroactive deployment of attention within working memory.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.bbr.2018.10.020.

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