Distractor inhibition contributes to retroactive attentional orienting within working memory: Evidence by lateralized event-related parameters of the EEG

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Abstract

Shifts of attention within mental representations based on retroactive cues (retro-cues) facilitate performance in working memory tasks. It was suggested that this retro-cue benefit is related to the concentration of working memory resources on a subset of representations, thereby improving storage and retrieval at the cost of non-cued items. However, the attentional mechanisms underlying this updating of working memory representations remain unknown. Here, we present EEG data for distinguishing between target enhancement and distractor suppression processes in the context of retroactive attentional orienting. Therefore, we used a working memory paradigm with retro-cues indicating a shift of attention to either a lateralized or non-lateralized item. Posterior and anterior asymmetries in the event-related potential suggested a contribution of both target enhancement and distractor suppression to retroactive attentional selection. Following this stage of selection, there was an increase of posterior alpha power contralateral compared to ipsilateral to the irrelevant item when a non-lateralized mental representation was cued. No comparable asymmetry was revealed when a lateralized item had to be selected. This suggests that the inhibition of the non-cued information is an important feature of attentional orienting within working memory. The current results thus enable a first impression on the interplay of attentional sub-processes in the context of retroactive cuing.

Keywords: Working memory, attention, retro-cue, alpha oscillations, selective forgetting

1. Introduction

Working memory comprises functions that allow for the temporary storage of information in order to make it accessible for higher-level cognitive operations (Baddeley, 1996; Baddeley & Hitch, 1974). Goal-directed behavior under changing environmental conditions requires to keep only those mental representations in working memory that are relevant for current action. This entails shifting the focus of attention within working memory representations and focusing on certain representations at the expense of no-longer relevant information. By means of event-related parameters in the EEG, the current study investigated to what extent excitatory and inhibitory processes contribute to this orienting of attention on the level of working memory.

So-called retroactive cuing (or retro-cue) paradigms are a good way to study the allocation of attention within working memory. It could be shown that comparable to cues causing a shift of attention toward a subset of to-be-presented stimuli in a memory array, also those presented after encoding facilitate performance in visuo-spatial working memory paradigms (Griffin & Nobre, 2003; Oberauer, 2002; Schneider, Mertes, & Wascher, 2015; Souza & Oberauer, 2016). Here, we focus on the sub-processes that underlie attentional selection within visuo-spatial working memory representations. When speaking of 'selection', there are two potentially relevant mechanisms: Attentional templates for target features lead to a top-down bias on the firing of neurons coding for these features, thereby leading to a representational advantage in the course of visual processing (i.e. 'target enhancement'). Additionally, an attentional template might also function by turning down the response of neurons coding for non-relevant features. This can be mediated by top-down inhibitory mechanisms or by lateral inhibition from the attended feature (or both; Desimone, 1998; Desimone & Duncan, 1995).

For attentional selection in the course of perception, it could already be shown that both target enhancement and distractor inhibition play a prominent role. Hickey, DiLollo and McDonald (2009) studied attentional sub-processes in visual search by making use of lateralized responses in the EEG. As our visual system is retinotopically organized to large extents, the authors presented either distractor or target items on lateral positions in a visual search display. A prominent component in the event-related potential (ERP) of the EEG, the N2 posterior contralateral or N2pc (Luck & Hillyard, 1994a, 1994b), was thereby divided into a posterior contralateral negativity indexing target enhancement (target negativity or Nt) and a posterior contralateral positivity reflecting distractor inhibition (distractor positivity or Pd).

Retroactive attentional orienting within working memory was also shown to elicit retinotopically organized asymmetries in the EEG, in form of an N2pc-like effect, an anterior contralateral negativity in the ERP (i.e., anterior directing attention negativity or ADAN; Myers, Walther, Wallis, Stokes, & Nobre, 2015; Schneider, Barth, Getzmann, & Wascher, 2017; Schneider, Mertes, & Wascher, 2016) and a contralateral decrease in posterior oscillatory power in the alpha frequency range (Myers et al., 2015; Poch, Capilla, Hinojosa, & Campo, 2017; Poch, Carretie, & Campo, 2017; Schneider et al., 2016). We thus made use of the spatial separation of target and distractor stimuli and combined it with two retro-cue based working memory tasks in order to separate target enhancement and distractor inhibition processes. We presented a retro-cue indicating the relevant memory array item and further used a probe presented at the time of the retro-cue as a control condition. If retroactive attentional selection is based on target enhancement, we should observe a contralateral negativity in favor of the cued item when it was presented lateralized. However, if also distractor inhibition is involved, there should be a contralateral positivity when only the distractor is lateralized. In the same vein, a contralateral decrease in posterior alpha power with a lateralized target would indicate target enhancement, while an increase in alpha power contralateral to the non-cued item would point toward distractor inhibition on the level of working memory.

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 the experiment. All participants were right-handers. As shown by means of a screening questionnaire, none of them reported any known neurological or psychiatric diseases and had normal (non-corrected) vision. Participation was rewarded by a payment of 10 € per hour or course credit. All participants gave their informed consent for participation after receiving written information about the study's purpose and procedure. The studies were run 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 experiment was run on a 22-inch CRT monitor (100 Hz) with a viewing distance of 150 cm and a display resolution of 1024 x 768 pixels. Stimulus presentation was done by means of a ViSaGe MKII Stimulus Generator (Cambridge Research Systems, Rochester, UK). Throughout the whole trial, a black fixation cross was presented on a dark gray

background (luminance of 15 cd/m^2). Participants were instructed to always fixate. This was furthermore controlled by an SMI Red 500 eye-tracking device (SensoMotoric Instruments, Teltow, Germany) measuring eye-movements at a frequency of 120 Hz. Prior to the beginning of the experiment and after each experimental block (see below), eye tracking was calibrated by measuring eye movements while presenting a gray circle (25 cd/m^2) on a dark gray background (10 cd/m^2) that successively moved to five different positions. We defined a 2° x 2° (visual angle) area around the central position of the screen and fixation control during the experiment was then carried out by only starting a trial (i.e. presenting the initial memory array), when participants fixated for at least 40 ms within a 100 ms interval prior to the memory array. The intertrial interval was set to 500-1000 ms (randomized), but was extended by on average 409 ms (SD=198.72 ms) due to the fixation control procedure.

The memory array was composed of three bars (0.1 by 1° of visual angle; see figure 1) presented with a random orientation, under the premise 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 (i.e. on the horizontal median). The other two bars were presented above fixation and placed to the left and right side. One of these lateralized bars was presented in gray with 25 cd/m^2. The two remaining bars (lateralized position or central position below fixation) were also presented with 25 cd/m^2, but either in color red (CIE: 0.566, 0.376, 0.25) or blue (CIE: 0.168, 0.131, 0.25). Accordingly, only one of the two lateralized items was colored, while the contralateral bar was always presented in gray (see figure 1). While the gray bar was never relevant for task performance, the red and blue bars were potentially relevant until presentation of the subsequent retro-cue or memory probe. The memory array was presented for 200 ms and followed by the retro-cue or a memory probe with an inter-stimulus interval of 800 ms. In the retro-cue condition, the cue was presented as an enlarged fixation cross and indicated the relevant memory item by color (red or blue). In 2/3 of all retro-cue trials, the cued item was presented left or right of fixation (i.e. target lateralized condition). In the remaining trials, the retro-cue pointed toward the central item below the fixation cross, indicating one lateralized working memory representation as irrelevant (i.e. distractor lateralized condition). This condition was presented in only 1/3 of the retro-cue trials to present the target equally frequent at each memory array position. The retro-cue was presented for 100 ms and followed by a further delay interval of 900 ms. Afterwards, a randomly oriented black bar (0 cd/m^2) was presented at fixation and had to be matched in orientation to the previously cued item by moving the computer mouse. This memory probe

remained presented for 3000 ms. Participants were instructed to press the left computer mouse button when they considered their orientation adjustment as appropriate.

Insert figure 1 about here

We furthermore included an 'early probe' condition in 50% of the trials (see figure 1) as a control condition for estimating the retro-cue benefit in the current working memory task (Souza, Rerko, & Oberauer, 2016). In this condition, the retro-cue was replaced by the onset of the memory probe display that again remained visible for 3000 ms. The cued item was indicated by presenting the rotatable memory probe in either red or blue. The proportion of the target vs. distractor lateralized conditions was the same as in the retro-cue condition. Overall, the experiment consisted of 960 trials divided into 8 blocks of trials. A short break of two minutes was made between the blocks in order to prevent fatigue in the course of the experiment.

2.3. EEG recording and preprocessing

EEG was recorded from 64 Ag/AgCl passive electrodes (Easycap GmbH, Herrsching, Germany) affixed across the scalp according to the extended 10/20 System and with a frequency of 1000 Hz by means of a NeurOne Tesla AC-amplifier (Bittium Biosignals Ltd, Kuopio, Finland). A 250 Hz low-pass filter was used during recording. The ground electrode was set to midline electrode AFz. The reference electrode during recording was at FCz. Impedance was kept below 10kΩ during recording.

We used MATLAB® and EEGLAB (Delorme & Makeig, 2004) for analyzing the EEG data. A 0.5 Hz high-pass and 30 Hz low-pass filter were applied prior to re-referencing the data to the average signal of all channels (average reference) and rejecting bad channels. Channel rejection was based on an absolute threshold limit of 5 SD regarding the kurtosis measure for each channel. Data epochs were then created beginning 1000 ms before and ending 3000 ms after memory array presentation. Independent component analysis (ICA) was run on every second epoch in the dataset and ADJUST (Mognon, Jovicich, Bruzzone, & Buiatti, 2011) was used to detect ICs related to eye blinks, vertical and horizontal eye movements and generic data discontinuities. The IC weights of the dataset reduced to every second trial were then transferred to the whole dataset and the selected ICs were removed from the signal. Additionally, we computed single dipoles for each IC by means of a boundary element head model (Fuchs, Kastner, Wagner, Hawes, & Ebersole, 2002), and also excluded ICs 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).

3. Results

3.1. Behavioral data

The raw angular errors were calculated by subtracting the orientation set for the memory probe from the original orientation of the cued item in the memory array. Therefore, the largest possible angular error was 90°. As a further parameter for assessing working memory accuracy, we calculated the standard deviation (SD) of the raw error within each experimental condition. These values were adjusted for circular data by means of the CircStat Toolbox for MATLAB® (Berens, 2009). Regarding parameters reflecting the speed of response, we chose to measure both the onset of the computer mouse movement and the time of the button press. While the time point of the button press should also differ as a function of the difference in orientation between the cued item and the memory probe, the onset of computer mouse movement should provide a reliable measure of the time required for response preparation. Only trials with a mouse button press were included in the behavioral analyses. The rate of button presses across trials was 99.81% on average (SD=0.29%). Cohen's d_z for dependent measures is used as an indicator for effect size.

Insert figure 2 about here

No difference in behavioral performance between the retro-cue and the early probe conditions appeared regarding the raw error, $t(19)=-0.233$, $p=0.819$, $d_z=-0.052$, and SD of the raw error, $t(19)=-0.911$, $p=0.374$, $d_z=-0.204$, indicating that in our sample the retro-cue did not lead to an increase in the overall accuracy of the recalled working memory representations (see figure 2A). However, highly reliable differences were observed regarding the parameters reflecting the speed of response: For the time of the mouse button press (see figure 2B), $t(19)=-9.977$, $p<0.001$, $d_z=-2.231$, and to an even larger extent for movement onset (see figure 2C), $t(19)=-12.48$, $p<0.001$, $d_z=-2.791$, the retro-cue condition revealed faster responses compared to the early probe condition. This can be related to the fact that a reliable retro-cue allows for planning the response (i.e. the desired end point of the computer mouse movement) already ahead of memory probe onset (Myers, Stokes, & Nobre, 2017; Schneider, Barth, & Wascher, 2017).

In addition, the continuous performance response allowed for fitting a mixture model on the data that divided the response distribution into four parameters (Bays, Catalao, & Husain, 2009): Parameter Kappa (κ) reflects the precision of the recalled working memory

representation independent from the item focused on for recall. Parameters pT, pN and pU refer to the probabilities to report the target item (pT), the non-target item (pN) and the probability to report at random (pU). There was a trend toward a lower probability to report at random (pU) in the retro-cue compared to the early probe condition, $t(19)=-1.726$, $p=0.101$, $d_z=-0.386$. Parameter pT, $t(19)=1.571$, $p=0.133$, $d_z=0.351$, and also the remaining parameters did not reveal a difference between these conditions (all p-values > 0.56). Overall, these findings point toward behavioral benefits of the retro-cue that manifest in the speed of response but not in response accuracy.

3.2. EEG data

3.2.1. Event-related potentials

The contralateral vs. ipsilateral portions of the ERP were calculated for both the retro-cue and the early probe condition in a similar way. For trials with a lateralized target item, we averaged across left-sided channels and trials with cued memory items on the right side and right-sided channels and cued items on the left side (i.e. contralateral). The ipsilateral portion was accordingly calculated by averaging across trials with cued memory items on the right side and right-sided electrodes and cued memory items on the left side and left-sided electrodes. The same procedure was run based on the location of the non-cued item in the distractor lateralized condition. In accordance with prior research on lateralized ERP effects and working memory, this averaging was done based on a posterior cluster of lateral electrodes (PO7/8, PO3/4, P7/8, P5/P6; e.g. Ikkai, McCollough, & Vogel, 2010; Vogel & Machizawa, 2004) and an anterior cluster for measuring the ADAN effect (FC3/4, F3/4; e.g. Schneider et al., 2015, 2016).

In order to estimate time windows of interest for statistical analyses, we averaged across the retro-cue and early probe conditions. At posterior lateral sites, there was an early contralateral positivity when the distractor was lateralized. The latency of this effect was assessed by measuring the 50% fractional area latency or FAL (i.e., the time point when the area under a curve within a certain interval reaches 50%) regarding the 'positive area' under the grand average of the contralateral minus ipsilateral difference wave from 200 to 400 ms following the retro-cue or probe display (i.e., 262 ms FAL). The same procedure was run regarding the 'negative area' under the difference curve in the target lateralized condition (i.e., 315 ms FAL). Afterwards, the mean amplitudes of the contralateral and ipsilateral portions of the ERP were measured in a 100 ms interval centered at these latency values. To test for differences between experimental conditions a 2x2x2 within-subject ANOVA was run including the factors *asymmetry* (contralateral vs. ipsilateral referred to distractor or target),

cue-type (retro-cue vs. early probe) and *target position* (target lateralized vs. distractor lateralized). Partial eta squared (η_p^2) is given as an indicator of effect size. Post-hoc comparisons were Dunn-Sidak corrected. In this case, we provide the mean contralateral minus ipsilateral differences between the tested conditions (M_{diff}), the standard errors of these differences (SE_{diff}) and the respective *p*-values. As we intended to disentangle excitatory and inhibitory sub-processes of attentional selection, we were mainly interested in differences in the interactions including the *asymmetry* factor. It was shown that posterior asymmetries in the early time interval differed between the target lateralized and distractor lateralized conditions, $F(1,19)=30.271$, $p<0.001$, $\eta_p^2=0.614$. As shown in figure 3, there was a contralateral positivity in the distractor lateralized condition ($M_{diff}=0.153$ µV, $SE_{diff}=0.069$ µV, $p=0.04$), but a contralateral negativity in the target lateralized condition ($M_{diff}=-0.242$ µV, $SE_{diff}=0.07$ µV, $p=0.003$). Stronger posterior ERP asymmetries were observed for the early probe ($M_{diff}=-0.168$ µV, $SE_{diff}=0.063$ µV, $p=0.015$) compared to the retro-cue condition ($M_{diff}=0.078$ µV, $SE_{diff}=0.076$ µV, $p=0.315$), $F(1,19)=11.931$, $p=0.003$, $\eta_p^2=0.386$. However, there was no three-way interaction, $F(1,19)=1.496$, $p=0.236$, $\eta_p^2=0.073$, indicating that the differences in posterior asymmetries between the distractor and target lateralized conditions did not differ between the early probe and retro-cue conditions.

Insert figure 3 about here

Also at the anterior lateral sites, there was a contralateral positivity for the distractor lateralized condition and a contralateral negativity for the target lateralized condition (see figure 4). In line with earlier studies indicating a later peak of the ADAN effect referred to the early posterior asymmetries in the ERP (Schneider et al., 2015, 2016), the latencies of the anterior effects were measured in a time window from 300 to 600 ms following the retro-cue or probe display (distractor lateralized: 396 ms; target lateralized: 396 ms). The ANOVA based on 200 ms mean amplitude intervals (see above) supported that a positive deflection in the contralateral minus ipsilateral difference wave was shown in the distractor lateralized condition ($M_{diff}=0.264$ µV, $SE_{diff}=0.052$ µV, $p<0.001$), while a negative deflection was shown for the target lateralized condition ($M_{diff}=-0.33$ µV, $SE_{diff}=0.054$ µV, $p<0.001$), $F(1,19)=66.983$, $p<0.001$, $\eta_p^2=0.779$ (see figure 4). The anterior asymmetry did not differ between the retro-cue and early probe conditions, $F(1,19)=0.051$, $p=0.823$, $\eta_p^2=0.003$, and also the *asymmetry x cue-type x target position* interaction was not significant, $F(1,19)=0.818$, $p=0.377$, $\eta_p^2=0.041$.

Insert figure 4 about here

Furthermore, both the target lateralized and distractor lateralized conditions indicated a late contralateral positivity over posterior sites. We measured the latency of these effects as the 50% FAL regarding the 'positive area' under the contralateral minus ipsilateral difference curves from 400 to 1000 ms following the retro-cue or probe displays (distractor lateralized: 646 ms; target lateralized: 600 ms). The ANOVA based on 200 ms mean amplitude intervals centered on these latencies indicated a marginal interaction between asymmetry and cue-type, $F(1,19)=3.825$, $p=0.065$, $\eta_p^2=0.168$. Post-hoc comparisons proved that the late contralateral positivity was shown in the early probe condition ($M_{diff}=0.265$ µV, $SE_{diff}=0.089$ µV, $p=0.007$), but was not evident following a retro-cue ($M_{diff}=0.076$ µV, $SE_{diff}=0.051$ µV, $p=0.15$). The late posterior contralateral positivity did not differ between the target lateralized and distractor lateralized conditions, $F(1,19)=0.176$, $p=0.68$, $\eta_p^2=0.009$, and also the three-way interaction *asymmetry x cue-type x target position* was not significant, $F(1,19)=0.789$, $p=0.386$, $\eta_p^2=0.04$.

In summary, these analyses suggest that both the lateralized target and the lateralized distractor contributed to the emergence of early posterior and anterior asymmetries. While the lateralized distractor was related to a contralateral positivity over posterior and anterior sites reflecting an inhibitory process, target selection was associated with a posterior and anterior contralateral negativity. The late posterior contralateral positive complex appeared only in the early probe condition, but independent from target position. This might suggest that it reflected a rather basic process related to the guiding of the motor response required in the early probe condition.

3.2.2. Event-related spectral perturbation

Spectral power or event-related spectral perturbation (ERSP; Delorme & Makeig, 2004) was computed by convolving three-cycle complex Morlet wavelets with each epoch of the EEG data. Epochs consisted of 200 time points from -1000 to 3000 ms referred to the memory array and frequencies ranged from 4 to 30 Hz in 52 logarithmic steps. The number of cycles used for the wavelets increased half as fast as the number of cycles in the respective fast-fourier transformation (FFT). This resulted in 3-cycle wavelets used for 4 Hz and 11.25-cycle wavelets used for 30 Hz.

Insert figure 5 about here

The posterior lateral electrodes PO7/8, PO3/4, P7/8 and P5/6 were considered for further analyses. As it was not possible to define the analysis time windows and frequencies of interest a priori, we first calculated the contralateral vs. ipsilateral portions of the ERSPs

(see above) and then averaged across the retro-cue and the early probe conditions. Attentional modulations in the ERSPs were then assessed by comparing the contralateral minus ipsilateral difference by means of within-subject *t*-tests between the target lateralized and distractor lateralized conditions for each ERSP data point. These tests were corrected for multiple comparisons by means of the false discovery rate (FDR) procedure (Benjamini & Hochberg, 1995). As shown in figure 5, these analyses revealed a significant cluster with increased contralateral vs. ipsilateral spectral power for the distractor lateralized compared to the target lateralized condition. The cluster appeared in the alpha frequency range (10-12 Hz) at about 430 ms to 600 ms following the retro-cue or probe display. Further analyses were based on these time and frequency ranges. An ANOVA was run including the within-subject factors *asymmetry* (contralateral vs. ipsilateral), *target position* (distractor lateral vs. target lateral) and *cue-type* (retro-cue vs. early probe). There was a main effect of *cue-type*, $F(1,19)=32.456$, $p<0.001$, $\eta_p^2=0.631$, indicating a higher alpha power suppression over posterior sites for the early probe compared to the retro-cue condition. While the main effects of target position, $F>1$, and asymmetry, $F(1,19)=2.013$, $p=0.172$, $\eta_p^2=0.096$, were not significant, there was a reliable interaction of these factors, $F(1,19)=37.397$, $p<0.001$, $\eta_p^2=0.663$. This interaction was based on a contralateral vs. ipsilateral increase in alpha power for the distractor lateralized condition ($M_{diff}=0.291$ dB, $SE_{diff}=0.078$ dB, $p=0.001$) and the absence of a reliable asymmetry effect in the target lateralized condition, ($M_{diff}=-0.094$ dB, $SE_{diff}=0.075$ dB, $p=0.225$) (see figure 5). The retro-cue and the early probe conditions did not differ regarding this interaction of *asymmetry* and *target position*, $F(1,19)=1.167$, $p=0.293$, $\eta_p^2=0.058$. 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.

4. Discussion

The current study investigated the contribution of target enhancement and distractor suppression mechanisms to retroactive attentional orienting. In a delayed estimation working memory paradigm, a retro-cue or memory probe indicated either a lateralized item (i.e. target lateralized condition) or non-lateralized item from a bilateral memory array (i.e. distractor lateralized condition) for report. Results suggest that both attentional sub-processes play an important role in retroactive attentional orienting, but manifest in different parameters of the EEG.

On behavioral level, retro-cues led to a performance benefit compared to the early probe condition (see figure 2). While there was no reliable difference between these conditions

based on the accuracy and mixture model parameters, responses were faster in the retro-cue compared to the early probe condition. This effect was observed both for the response onset time (i.e. the time between probe onset and the first computer mouse movement) and the time required to complete the rotation movement (i.e. the button press). This suggests that retro-cues led to the faster completion of response preparation, a finding that is in line with earlier observations on a head-start of item retrieval and response planning mechanisms following a reliable retro-cue (Myers et al., 2017; Schneider, Barth, & Wascher, 2017; Souza et al., 2016). While in the early probe condition the retrieval of the cued item and the processing of the probe had to proceed simultaneously, the retro-cue allowed to select the cued mental representation ahead of the probe information and already transfer it into a response-oriented representational state (i.e. response planning). An earlier study by Souza and colleagues (2016) also found a retro-cue benefit on accuracy level compared to an early probe condition. However, in this study, the set size in the initial memory array containing differently colored items was six. It can be assumed that the focusing on one out of two memory representations in the current study did not suffice for revealing reliable retro-cue benefits on the level of accuracy.

The separation of attentional sub-processes during retroactive attentional orienting was based on lateralized effects in the EEG. On ERP level, a prolonged contralateral negativity with a maximum over posterior sites emerged following the initial memory array. This so-called contralateral delay activity (CDA; see Vogel & Machizawa, 2004) emerged due to the potentially relevant item presented on the left or right side of central fixation. There was no reliable modulation regarding the amplitudes of posterior P1 and N1 elicited by the retro-cue or probe display. Following this sensory processing stage, the contralateral and ipsilateral portions of the ERP indicated posterior and anterior asymmetries in the retro-cue and early probe conditions. There was an early posterior positivity contralateral to the lateralized distractor and a posterior negativity contralateral to the lateralized target. The figures suggest that the distractor positivity (Pd) effect was mainly driven by the retro-cue condition, while the target negativity effect (or Nt; see Hickey et al., 2009) was rather evident in the early probe condition. However, it has to be noted that we did not observe a significant three-way interaction in this regard. This does not allow for a statement on different attentional mechanisms triggered by these cue-types.

The early posterior asymmetry in the ERP overlapped in time with an anterior asymmetry that was previously referred to as anterior directing attention negativity or ADAN. ADAN was described to reflect a higher-level control mechanism for shifting the focus of

attention in perceptual space (Eimer, van Velzen, & Driver, 2002) and also within mental representations (Schneider, Barth, Getzmann, et al., 2017; Schneider et al., 2015, 2016). Our data indicate that ADAN, just like the posterior asymmetry, can be divided into two attentional sub-processes: The retroactive orienting of the attentional focus was related to an increased contralateral vs. ipsilateral negativity. The frontal topography of this asymmetry also suggested a contribution of residual eye movements to the observed effects. However, there was also an anterior positivity contralateral to the irrelevant item that cannot be related to saccadic eve movements toward a non-lateralized target (see figure 4). Thus, target selection obviously required a higher-level control process for inhibiting the non-cued representation, reflected by the anterior contralateral positivity. In combination with the posterior asymmetries, these findings indicate that the attentional control processes on perceptual level (e.g. in visual search) and within visuo-spatial working memory are highly similar: The control mechanisms act by means of excitatory and inhibitory modulations on the retinotopic representations within posterior areas (Nt and Pd), but also on higher-level frontal representations.

We can thus summarize that attentional selection in working memory includes both the focusing on relevant information and the inhibition of the irrelevant or distracting representations. However, up to this point, the results do not allow for a statement on the consequences of these mechanisms. Does attentional selection within working memory contents necessarily lead to the 'forgetting' of the non-cued representations, or is it exclusively related to the transfer of the cued representation into a higher-level representational state? Here, we propose a cascade of processes involved in retroactive attentional orienting based on a further lateralized effect in the EEG: posterior asymmetries in alpha power. Several studies investigated the lateralization of posterior alpha power as an indicator for retroactive attentional orienting (e.g. Myers et al., 2015; Poch, Campo, & Barnes, 2014; Poch, Capilla, et al., 2017; Poch, Carretie, et al., 2017; Schneider et al., 2016). Comparable to the current experiment, Poch and colleagues (2017) presented endogenous color retro-cues toward memory items presented on the left or right side of fixation and revealed a higher decrease in alpha power contralateral compared to ipsilateral to the cued contents. This effect was not sustained throughout the delay period and was thus associated with a temporary attentional process rather than working memory storage. The lateralization of alpha power in the context of attentional orienting was interpreted as the consequence of an inhibitory control process setting the neural population processing irrelevant signals into a kind of 'idling state'. This state goes along with an increase in alpha power contralateral to

irrelevant or distracting information (Handel, Haarmeier, & Jensen, 2011; Kelly, Lalor, Reilly, & Foxe, 2006; Klimesch, 2012; Rihs, Michel, & Thut, 2007; Sauseng et al., 2005). However, recent studies in the field of working memory rather favored the notion that alpha suppression is related to target processing (Fukuda, Mance, & Vogel, 2015; Myers et al., 2015). The current study is the first that strictly distinguishes between target enhancement and distractor inhibition processes on the level of lateralized alpha power in a retro-cue task. We show that in a time window following the early posterior ERP asymmetries, there was an increase in alpha power contralateral compared to ipsilateral to a distractor item, but no alpha asymmetry when the target item was presented lateralized. It can thus be assumed that a first phase reflecting retroactive attentional selection (Nt, Pd and ADAN) was followed by a further attentional process related to the dealing with the irrelevant mental representation. There are two possible ways this dealing with the irrelevant item or distractor might proceed: A lateralization of posterior alpha power might reflect a control process for actively inhibiting the irrelevant mental representation or it might be the consequence of an automatic 'letting go' of the distractor representation. In both cases, retroactive attentional orienting should lead to a change of the irrelevant representation into a more passive and fragile short-term memory state (e.g. Sligte, Scholte, & Lamme, 2008; Vandenbroucke, Sligte, de Vries, Cohen, & Lamme, 2015; Vandenbroucke, Sligte, & Lamme, 2011), while leaving the target item within the focus of attention in working memory. Or in other words, posterior alpha lateralization in a retro-cue task is rather associated with changes of the representational status of irrelevant contents than with enhancing the target representation.

In future projects, it might be possible to dissociate active and passive forgetting in working memory by also presenting cues indicating which representation to forget (Williams, Hong, Kang, Carlisle, & Woodman, 2013; Williams & Woodman, 2012). If such forget cues facilitate the posterior alpha lateralization regarding lateralized distractors compared to remember cues, this would speak in favor of active forgetting within working memory.

In summary, the current study provided first insights into the attentional sub-processes underlying the updating of visuo-spatial working memory representations. Retro-cues allowed for target selection and response planning ahead of the presentation of the memory probe, thereby leading to faster responses in a delayed estimation working memory task compared to the early probe condition. Attentional selection based on the retro-cues or probes was investigated by means of lateralized effects in the ERP and in oscillatory power. Comparable to attentional selection in the course of perception, retroactive attentional selection was associated with posterior and anterior asymmetries in the ERP that were composed of

mechanisms related to target selection and those related to distractor inhibition. Following this selection process, we observed an increase in posterior alpha power contralateral compared to ipsilateral to the distractor item. It can thus be assumed that the alpha lateralization following retro-cues in earlier studies (e.g. Myers et al., 2015; Poch, Capilla, et al., 2017; Poch, Carretie, et al., 2017; Schneider et al., 2015, 2016) was related to changes in the representational state of the non-cued working memory contents and not to a modulation of the relevant mental representations. The behavioral benefit of retro-cues in working memory tasks should thus to large extents be related to the efficiency in dealing with the no longer relevant information.

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7. Figures

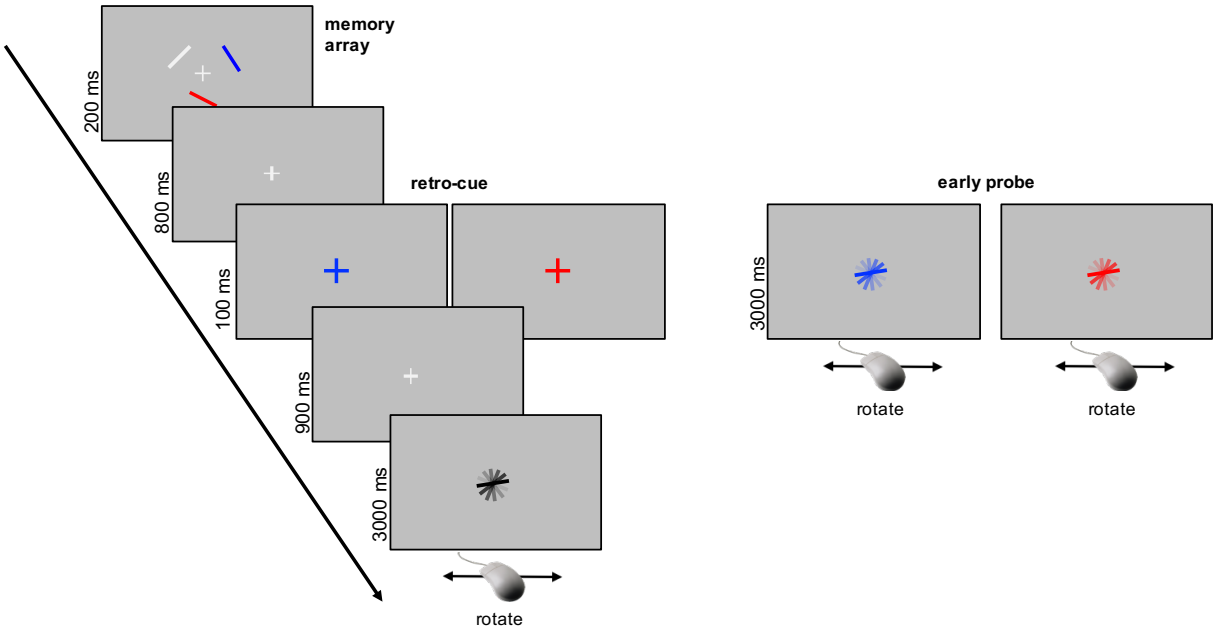

Figure 1. Experimental design. Each trial featured an initial memory array containing two potentially relevant randomly oriented bars (blue and red) and one irrelevant bar (gray). The irrelevant bar was always presented on a lateral position. A subsequent retro-cue or early probe indicated either the lateralized or non-lateralized (bottom) stimulus as relevant for the orientation adjustment task.

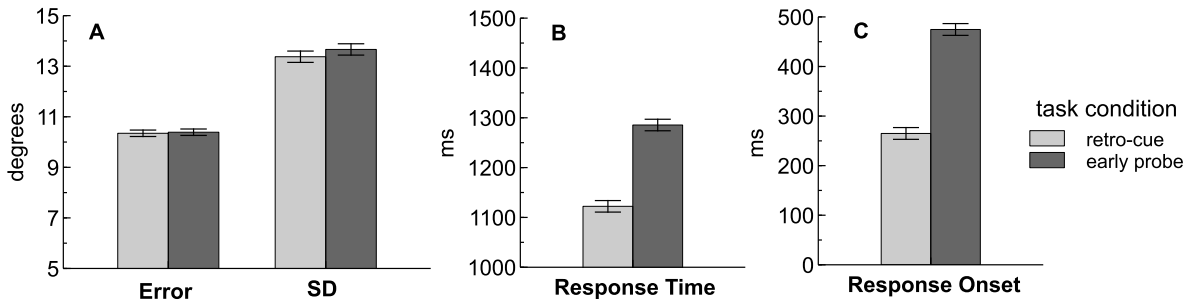

Figure 2. Behavioral data. Task accuracy was defined as the raw angular error between the cued item from the memory array and the adjusted orientation. No difference in performance between the retro-cue and early probe condition was shown on the level of the raw error and the standard deviation (SD) of the raw error (**2A**). However, participants were faster in task completion (i.e. time until computer mouse button press; **2B**) and in starting the orientation adjustment (i.e. response onset time; **2C**) in the retro-cue compared to the early probe condition. Error bars reflect the standard error of the mean.

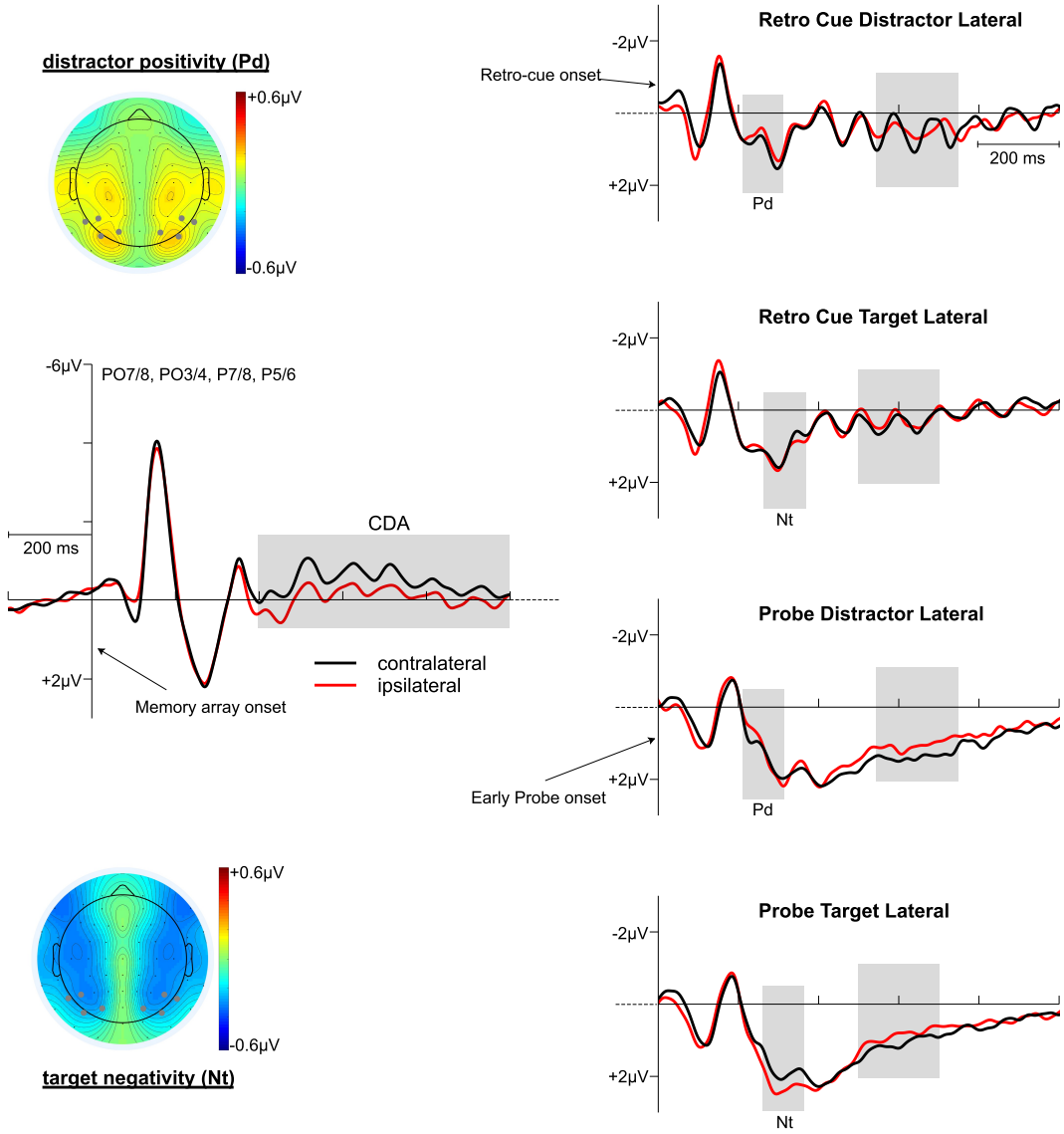

Figure 3. Posterior asymmetries in the ERP (PO7/8, PO3/4, P7/8, P5/6). The phase from memory array presentation to retro-cue onset is displayed averaged across all experimental conditions. The right-sided plots indicate the retro-cue condition (**3A-B**) and the early probe condition (**3C-D**) with a lateralized target (**3A, 3C**) and a lateralized distractor (**3B, 3D**). The time intervals used for statistical analyses are marked by the gray squares overlaying the ERPs. Furthermore, we provide contralateral minus ipsilateral difference topographies in the time windows of the Pd and Nt effects (depicted on both hemispheres with zero values on the midline) for the target lateralized and distractor lateralized conditions averaged across the retro-cue and early probe conditions. The electrode positions chosen for statistical analyses are marked in gray.

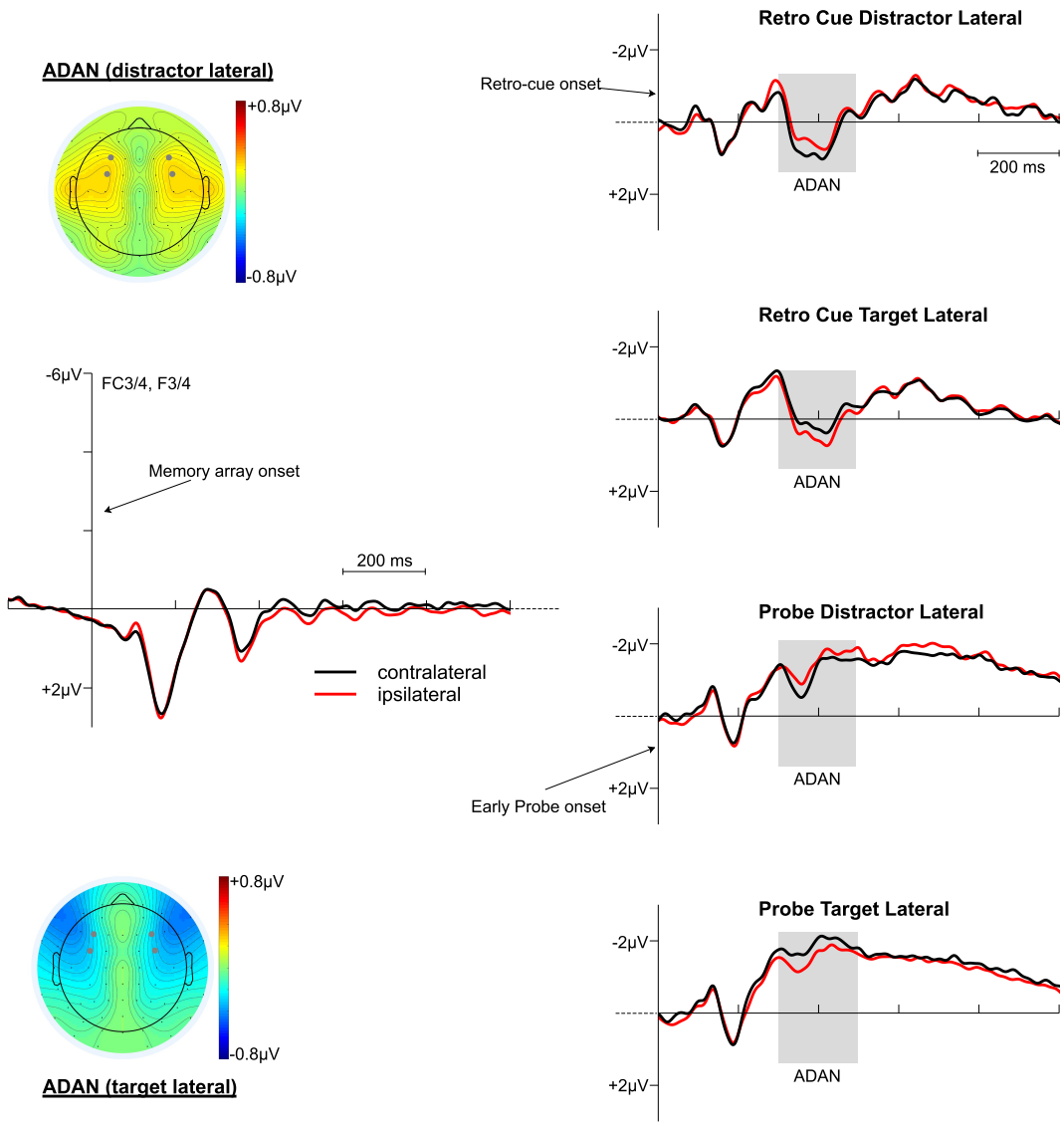

Figure 4. Anterior asymmetries in the ERP (FC3/4, F3/4). The phase from memory array presentation to retro-cue onset is displayed averaged across all experimental conditions. The right-sided plots indicate the retro-cue condition (**4A-B**) and the early probe condition (**4C-D**) with a lateralized target (**4A, 4C**) and a lateralized distractor (**4B, 4D**). The time intervals used for statistical analyses are marked by the gray squares overlaying the ERPs. We further provide contralateral minus ipsilateral difference topographies in these time windows (depicted on both hemispheres with zero values on the midline) for the target lateralized and distractor lateralized conditions averaged across the retro-cue and early probe conditions. The electrode positions chosen for statistical analyses are marked in gray.

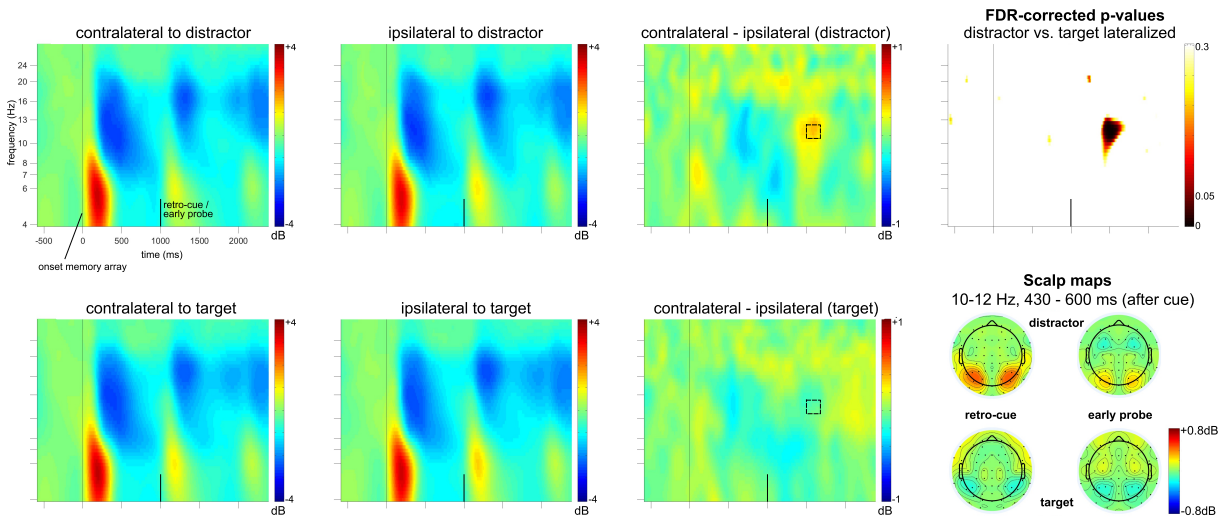

Figure 5. Lateralized effects in posterior ERSPs. The oscillatory responses following the memory array (vertical line at zero) are shown contralateral vs. ipsilateral to a distractor (upper row) and target item (lower row) at a posterior lateral electrode cluster (PO7/8, PO3/4, P7/8, P5/6). The contralateral minus ipsilateral ERSP difference as well as the FDR corrected t-tests on the comparison of the target and distractor lateralized conditions indicated an effect in higher alpha frequency range at about 430 to 600 ms following the retro-cue and early probe displays. As also indicated in the respective contralateral minus ipsilateral difference topographies, this effect was related to higher alpha power contralateral compared to ipsilateral to the lateralized distractors.