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Research report

# Searching for auditory targets in external space and in working memory: Electrophysiological mechanisms underlying perceptual and retroactive spatial attention



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#### ARTICLE INFO ABSTRACT Keywords: Attention can be shifted within internal representations maintained in working memory. These retroactive Auditory working memory processes are particularly inherent to the processing of auditory information that is especially transient over time Spatial attention and thus, requires us to continuously maintain, attend to, and integrate information in working memory. Using Retroactive attention EEG recordings, the present study investigated the neurophysiological mechanisms underlying selective spatial Auditory search attention in a retroactive as opposed to a perceptual auditory search task. Two kinds of sound stimuli were Alpha lateralization employed: a horizontal sound array consisting of two natural sounds presented simultaneously in the left and EEG right hemispace and a central single target sound. The target sound was provided either after (retroactive search) or before the presentation of the sound array (perceptual search). In both search conditions, participants completed a sound localization and a sound detection task, indicating the position (left or right) or the presence versus absence (yes or no) of a particular target sound. Analyses revealed a lateralization of alpha power oscillations (8-12 Hz) over parieto-occipital scalp in both perceptual and retroactive sound localization tasks, but not in respective sound detection tasks, suggesting auditory alpha lateralization to be restricted to spatiallyspecific task demands. The observed asymmetric modulations of alpha power in sound localization are consistent with analogous findings from the visual domain, supporting the supramodal role of alpha oscillations in the deployment of spatial attention. Hence, we conclude that auditory alpha lateralization is a higher-order attention

mechanism that operates in perceptual and mnemonic space reflecting the access to a spatially-specific, supramodal response template.

# 1. Introduction

While working memory and attention have been studied as distinct entities for decades, recent research has highlighted that there is a substantial overlap between the two, regarding both functional and anatomical principles [1,2]. In particular, the capacity to selectively focus on mental representations in working memory, a process termed retroactive [3,4] or reflective [5,6] attention, has received a surge of interest in the past decade. It has been shown that retroactive attention cues ("retro-cues") can direct attention towards a particular mental representation and thereby lead to a performance benefit during a subsequent memory task [7,8; for a review, see 9]. Usually, retro-cues provide information about the relevance of a subset of items in working memory for an upcoming task and thus, prompt the updating of working memory contents. By immediately prompting the retrieval of the cued item, post-cues can similarly induce the top-down attentional access to working memory representations [10,11]. Such retroactive processes appear particularly inherent to auditory processing, for instance, in language comprehension that requires us to continuously maintain, attend to, and integrate auditory information in working memory in order to form a coherent representation of what was heard [12].

Despite its implications for auditory perception, retroactive attention has been almost exclusively investigated in the visual domain and the neural underpinnings of auditory retroactive attention remain largely unknown. Findings from the visual domain have shown that attentional selection of a lateralized stimulus from representations held in working memory elicit a neurophysiological response similar to that associated with attentional selection from a perceptual array in external space [13–16]. For instance, a growing body of evidence suggests that the lateralization of parieto-occipital alpha oscillations (8–12 Hz), that has been shown to present a reliable marker of spatial attention, can be

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found in both internal [17-20] and external visual attention paradigms [21-24]. In the present study, we directly compared the modulation of alpha power oscillations in a retroactive and a perceptual auditory search task. Participants were asked to either detect or localize a specific target sound within a horizontal sound array that consisted of two simultaneously presented sounds, lateralized to the left and right hemispace. Depending on the search type, the target was defined before (pre-cue in the perceptual search task) or after (post-cue in the retroactive search task) the presentation of the sound array. The design addressed two overarching questions: (1) Is attentional orienting within perceptual auditory space and auditory working memory representations based on a comparable modulation of posterior alpha power? (2) Does auditory search for non-spatial features (i.e., sound detection) involve spatially-specific mechanisms of attentional orienting, that is, alpha power lateralization, as found in auditory search for spatial features (i.e., sound localization)?

The lateralization of parieto-occipital alpha rhythms is typically observed in terms of a decrease in alpha-band oscillations in the hemisphere contralateral to the attended target [23,25,26] or an increase of alpha power in the ipsilateral hemisphere [24,27-29]. Such hemispheric alpha lateralization is typically interpreted as a functional inhibition of irrelevant stimuli [21,28,30,31] or an enhanced processing of targets [21,23,26]. A wealth of studies has reported alpha lateralization in visual spatial [21-24] and retroactive cueing tasks [3,17-20], suggesting the involvement of analogous mechanisms underlying the attentional orienting in external (perceptual) and internal (mnemonic) visual space. Only recently, the involvement of alpha oscillations in auditory spatial attention has been examined in a handful of studies [32–35], suggesting that the respective auditory mechanisms may indeed operate in a highly comparable fashion or may even be based on a common supramodal control mechanism. More specifically, the existing spatial cueing studies, in all of which attention is directed to a particular lateralized external location in anticipation of a sound stimulus [32,34,36,37], concordantly reported a pattern of parieto-occipital alpha power lateralization that is highly similar to what has been found in analogous visual attention studies [21,22,24]. Supporting the hypothesized inhibitory function of lateralized alpha power, tACS stimulation at frequencies in the alpha range (10 Hz) over auditory and parietal cortex regions has been shown to impair the recall of auditory targets contralateral to stimulation [35]. So far, studies reporting alpha power modulations associated with the retroactive deployment of auditory attention to working memory representations remain scarce [38,39] and have primarily focused on the contrast between different types of retro-cues (valid vs. neutral, spatial vs. semantic) instead of lateralized modulations of alpha power. We propose that, if there is a higher-order supramodal system controlling the deployment of attention in both internal and external space, lateralized alpha suppression mechanisms comparable to those found in equivalent visual attention tasks, should also be evident during the perceptual and retroactive task in the present auditory search paradigm.

In the visual domain, spatial and non-spatial features are closely bound together [40,41], and irrespective of whether space is a taskrelevant dimension the access to non-spatial information is accompanied by a shift of spatial attention [13,42]. Hence, attending to a lateralized visual stimulus rather automatically involves the processing of its location. In contrast, in the auditory domain spatial information is less prioritized. Due to the primarily tonotopic organization of the auditory system, the spatially-specific processing of auditory stimuli requires extensive computations, based on monaural and binaural spectral cues, such as interaural timing differences [43]. Thus, the question arises, whether attentional selection in auditory internal or external space is necessarily associated with spatially-specific processing of the target sound. The distinction between sound detection and sound location in the present design allows us to reveal potential disparities in the underlying attentional processes associated with purely featurebased (i.e., spatially-unspecific sound detection) and spatially-specific (i.e., sound localization) task demands. Critically, the initial search for the target was always based on the knowledge of the target identity (feature-based search), but only the sound localization task required a spatially-specific response. Considering that attaining a spatially-specific representation of a given auditory stimulus requires additional computational effort, we speculate that auditory information is only transformed into a spatiotopic format when the task demands the selection of a spatially-specific response; lateralized auditory alpha modulations should therefore only occur in sound localization, but not in sound detection.

Taken together, the present study aims at the neurophysiological mechanisms related to attentional orienting during perception and within working memory representations and intends to establish a deeper understanding of the spatially-specific mechanisms of attentional deployment in the auditory domain.

# 2. Methods

## 2.1. Participants

Sixteen subjects ( $M_{age} = 25.5$ , age range = 21–30 years, 8 female) participated in the study. Inclusion criteria required normal or corrected-to-normal vision, no history of neurological or psychiatric disorders, right-handedness, and non-clinical hearing thresholds ( $\leq 25 \text{ dB}$  hearing level for frequencies from 0.125 to 4 kHz). The latter was tested conducting a standard pure tone audiometry (Oscilla USB 100, Inmedico, Lystrup, Denmark) prior to the experiment. All subjects gave their informed consent for participation after receiving written information about the study's purpose and procedure. As monetary compensation for the time invested, subjects received a payment of 10 Euros per hour. The experimental procedure was approved by the Ethical Committee of the Leibniz Research Centre for Working Environment and Human Factors and conducted in accordance with the declaration of Helsinki.

# 2.2. Materials and stimuli

Eight familiar animal sounds ('birds chirping', 'dog barking', 'frog croaking', 'sheep', 'cat meowing', 'duck quacking', 'cow mooing', 'rooster crowing') were chosen from an online sound archive [44]. Since the original sound files were of unequal duration, all sounds were cut to a constant duration of 600 ms (with a 10 ms on/off ramp) using the software Cool Edit 2000 (Syntrillium Software Corporation, Phoenix, AZ, USA). The spectro-temporal characteristics were left unchanged. Each trial consisted of one sound that was presented in isolation from a central position  $(0^{\circ})$  and two sounds that were presented simultaneously from lateralized azimuthal positions ( $\pm 40^{\circ}$ ). All sounds were presented using over-ear headphones (AKG K-271 Studio headphones). Virtual sound locations were generated using head-related transfer-function (HRTF) filter coefficients [44, for a detailed description of the method, see 46] recorded using a KEMAR (Knowles Electronic Mannequin for Acoustig Research) dummy head microphone. While sounds played via headphones are usually perceived to originate from inside of the head, the use of HRTFs allows for an externalized perception of the sound stimuli [45,47]. A total of 56 different two-sound arrays were created from the original eight sound stimuli, with each sound array presented up to 4 times per condition. Each of those sound arrays was randomly combined with one of the eight single target sounds so that all target sounds were presented equally often per condition, resulting in a series of sound sequences that was kept constant across all participants. The order in which single and two-sound files were presented was dependent on the search type (retroactive or perceptual search; cf., 2.3 Procedure and task). The average sound level of the individual sounds was 58.6 dB(A). Thus, the overall sound level increased slightly when two sounds were presented simultaneously (i.e., 64.5 dB(A)).

## 2.3. Procedure and task

Throughout the experiment, a target sound and a lateralized sound array containing two concurrent sounds were presented (cf., 2.2 Materials and stimuli). Participants were required to either state whether the target sound was present or absent (1/2 of trials each; detection)task) or report its location (1/3rd left, 1/3rd right) within the sound array (localization task). In order to prevent participants from strategically attending to only one ear, localization task blocks also included sound arrays that did not contain the target sound (1/3rd target-absent trials). Otherwise, a participant attending to, for example, the left ear would have been able to infer the target position; that is, the participant would have known that the target was presented on the right side, simply because the target was not detected on the attended left side. In perceptual task blocks, the target sound was presented before the sound array. Thus, participants were aware of the relevant sound in advance and then searched through the perceptual sound array. In retroactive task blocks, the sound array was presented first, followed by the target sound. Consequentially, participants had to maintain the sound array in working memory until they were given information about the target. Taken together, the described experiment was based on a  $2 \times 2$  factorial repeated-measures design including the factors Task (localization, detection) and Search Type (perceptual, retroactive). The order of the four task blocks was counterbalanced across participants. To minimize fatigue, short rest-periods of approximately 2 minutes were provided inbetween task blocks.

At the beginning of each block, participants familiarized with the task in the course of ten practice trials. Task instructions were given prior to each task block with accuracy and speed equally emphasized. Each trial started with a randomized variable silent interval (500-800 ms). In perceptual search trials, the centrally presented target sound was followed by a silent inter-stimulus-interval (ISI) of 1000 ms and the lateralized two-sound array (Fig. 1). In retroactive search trials, the lateralized two-sound array was initially presented, followed, after a 1000 ms ISI, by the centrally presented target sound. The next trial was initiated self-paced, that is, with the participants' response. If no response was given within a maximum response period of 3000 ms, the next trial started automatically. Participants were instructed to continuously fixate a black fixation cross (0.5° visual angle) that was presented in the center of the computer screen throughout the whole experiment. With the response, the fixation cross disappeared for 200 ms to indicate the beginning of a new trial. In localization trials, subjects responded by pressing one of three keys on a vertically arranged response pad, using their right middle finger, index finger, and thumb. In

# (A) Perceptual search:



detection trials, only two response alternatives were given, that is, the key pressed by the middle finger was omitted. The assignment of response keys was counterbalanced across participants. In total, there were 672 trials with 288 localization trials (i.e., 48 target-left trials, 48 target-right trials, and 48 target-absent trials per search condition) and 384 detection trials (i.e., 48 target-left trials, 48 target-right trials, and 96 target-absent trials per search condition).

Please note that the original experiment included a load manipulation (i.e., an additional four-sound array) that was presented in a block-wise manner. These conditions are excluded here for the majority of participants were not able to perform substantially above chance level in the retroactive search conditions including a four-sound array.

# 2.4. Data analysis

Behavioral data, as well as EEG data, were analyzed using customwritten R scripts [48]. For all reported F- and t-statistics, partial eta squared ( $\eta_p^2$ , [49]) and Hedges' g<sub>av</sub> [50] are provided as measures of effect size, respectively. In case of significant violations of sphericity (Mauchly's test; p < .05), Greenhouse-Geisser correction was applied. Post-hoc comparisons were conducted by means of dependent sample *t*tests. Respective *p* values were FDR-corrected for multiple comparisons when appropriate [51].

### 2.4.1. Behavioral data

To quantify participants' performance in the perceptual and the retroactive auditory search task, mean reaction times and mean accuracy (percentage of correct trials) were assessed. Reported errors did not include omitted responses (i.e., no response was given within 3000 ms), since the majority of subjects responded to all trials (9 participants) or omitted only one or two trials (5 participants). On average, the percentage of trials without a response was 0.20% per subject (range = 0.15-1.79%, standard deviation = 0.43). To test for behavioral effects of Task (localization vs. detection) and Search Type (perceptual vs. retroactive), a repeated-measures analysis of variance (ANOVA) was performed for reaction times and error rates.

# 2.4.2. EEG recording and processing

EEG data were recorded using a 64-channel ActiCap (Brain Products, Gliching, Germany) system. The Ag/AgCl active electrodes were distributed across the scalp according to the extended 10/20 system, including a ground (AFz) and a reference electrode (FCz). Data were sampled at a frequency of 1000 Hz (BrainAmp DC-amplifier). Electrode impedance was kept below 10 k $\Omega$  during recording. MATLAB

Fig. 1. Experimental design. In perceptual search blocks, participants were presented a single target sound (from a center position) followed by a sound array containing two simultaneously presented sounds ( $\pm$  40°). In retroactive search blocks, the sound array was presented first, followed by a single target sound (from a center position). In a block-wise manner, participants were instructed to either indicate the position of the target sound (localization task) or the presence or absence of the target sound (detection task) via button press, resulting in a total of four task-blocks for each participant to be completed. Following the response, the fixation cross vanished for 200 ms and then reappeared to indicate the beginning of a new trial (not depicted). *ISI = inter-stimulus interval*.

(2016b), EEGLAB (v13.6.5b; [52]), and ERPLAB (v6.1.4; [53]) were used for further processing of the data. First, a 0.5 Hz high-pass offlinefilter (6601-point FIR filter; transition band width 0.5 Hz; cut-off frequency 0.25 Hz) and a 30 Hz low-pass offline-filter (441-point FIR filter, transition band width 7.5 Hz, cut-off frequency 33.75 Hz) were applied to the raw data. The continuous data files were then re-referenced to the average of all 64 electrodes and segmented into epochs from -1000to 4100 ms relative to the onset of the first sound stimulus (i.e., target sound in perceptual search trials and sound array in retroactive search trials). The resulting epochs were baseline-corrected using the 600 ms interval prior to the onset of the first sound file. In order to increase the signal-to-noise ratio, a semi-automatic artifact rejection procedure was applied: First, independent component analysis (ICA), based on a subset of the data (down-sampled to 200 Hz, every second trial) was run. Independent components (ICs) accounting for artifacts were identified and removed from the 'original' dataset (1000 Hz sampling rate) using the automatic algorithm ADJUST [54]. Additionally, single dipoles were fitted for each IC by means of a spherical head model implemented in the EEGLAB toolbox plug-in DIPFIT. ICs with a residual variance in the dipole solution exceeding the rejection threshold of 40% were excluded. A final visual inspection was conducted to ensure that all major artifact-related components were discarded. Remaining artifacts were removed using the automatic epoch rejection procedure as implemented in EEGLAB (threshold limit: 1000 µV, probability threshold: 5 SD). On average, 9.73% of trials (range: 3.13%-17.11%, SD = 3.91) were removed due to artifact rejection. Subsequently reported EEG-results include only correct responses that occurred within a time interval of 120 ms-1500 ms following the second sound stimulus (total of excluded trials = 681, mean percentage per subject = 6.94, range = 0.33-31.33, SD = 7.76). In addition, to assess the neural mechanisms of attentional deployment towards the auditory target, only target-present trials were included in further analyses.

# 2.4.3. Oscillatory activity

Event-related spectral perturbations (ERSP, cf., [52]) of the single trial data were computed by convolving the EEG-data with a three-cycle complex Morlet wave for frequencies from 6 to 30 Hz in 48 logarithmic steps. The number of cycles in the wavelets expanded as a function of frequency with a factor of 0.5 regarding the number of cycles in the corresponding fast Fourier transformation. This procedure resulted in three-cycle wavelets at the lowest frequency (i.e., 6 Hz) and 7.5-cycle wavelets at the highest frequency (i.e., 30 Hz). Epochs contained 300 ERSP time points and thus ranged from -721 ms and 3819 ms relative to the onset of the first sound stimulus. In addition, response-locked waveforms were created by re-segmenting the pre-processed data with the response as the time-locking event, creating epochs ranging from 2760 ms before and 1000 ms after the response. The response-locked ERSPs were computed based on the settings as described above, resulting in epochs containing 300 times points from 2481 before to 719 ms after the time-locking event.

To test for the effects of attentional deployment in working memory and perception on desynchronization in the alpha band (8-12 Hz), mean alpha power was measured at an electrode cluster over posterior scalp (i.e., four locations over each hemisphere, P5/P6, P07/8, P7/P8, and TP7/TP8). The choice of electrodes was based on scalp topographies and electrode selections in previous studies [25,28,31,55-58]. While electrode selections vary from study to study, we found the indicated scalp sites to be very frequently involved when topographies of alpha lateralization are investigated. In addition, prior reports of alpha lateralization show a substantial variation with respect to the measurement windows used [17,18,24,58-60]. Indeed, a direct comparison of a pre- and a retro-cue condition suggests that the lateralization of alpha power in the period prior to probe onset begins earlier in pre-cue trials than in retro-cue trials [58]. Thus, we assumed latency differences between the perceptual and the retroactive search condition. Consequently, in a first step, we assessed the 50% fractional area latency

(FAL<sub>50</sub>) to quantify the timing of alpha power modulations in both stimulus- and response-locked data. The FAL<sub>50</sub> refers to the point in time at which the negative area under the difference curve (i.e., the contralateral minus ipsilateral portions of alpha power) can be divided in two equal halves; thus, assessing the midpoint of the observed asymmetry. In the stimulus- and response-locked ERSPs, the negative area was assessed in a broad measurement window ranging from 200 to 1000 ms following to the second sound stimulus and from 500 ms before to 200 ms after the response, respectively. To reduce the impact of error variance when measuring the midpoint latency, a jackknife approach was chosen in this step of the analysis [61]. The latter creates 16 so-called 'leave-one-out' grand averages for each of the two search type conditions by successively averaging the data from all but one subject in the sample. Importantly, midpoint latencies for perceptual and retroactive search were measured from the ERSPs averaged across localization and detection blocks; thus, not considering the factor Task when determining the measurement windows. Differences between the assessed midpoint latencies were tested for significance using dependent sample t-tests. T-values were adjusted in accordance with Kiesel et al. [62]; *n* indicating the number of participants:

$$t = \frac{t}{n-1}$$

Finally, to investigate differences in alpha power amplitude between conditions, both in the stimulus- and response-locked data, mean alpha power was averaged separately across the contralateral and the ipsilateral portions of the signal (relative to the position of the target sound) in each condition. Mean values were obtained from a 200 ms time window around the FAL<sub>50</sub> for each search type. In case of a nonsignificant latency difference between perceptual and retroactive search, the 200 ms time window was based on the FAL<sub>50</sub> calculated from the grand average across all tasks (i.e., localization and detection) and search types (i.e., perceptual and retroactive search). Subsequently, the respective mean alpha power values for the stimulus- and responselocked data were submitted to two separate repeated-measures ANOVAs, each of which included the factors Asymmetry (contralateral vs. ipsilateral), Task (sound localization vs. sound detection), and Search Type (perceptual vs. retroactive). Electrode position was not included as an ANOVA factor to reduce the familywise error rate; thus, data were averaged across the electrode sites of interest.

#### 3. Results

### 3.1. Behavioral data

Mean reaction times (RT) and error rates (ER) are depicted in Fig. 2. The analysis of error rates revealed a diminished performance in retroactive search trials (mean ER = 10.55%, SE = 3.70) compared to perceptual search trials (mean ER = 4.39%, SE = 1.82), F (1,15) = 17.06, p = .0009,  $\eta_p^2 = 0.53$ , as well as an overall lower performance in sound localization trials (mean ER = 9.29%, SE = 3.83) compared to sound detection trials (mean ER = 5.65%, SE = 2.12), F (1,15) = 13.44, p = .002,  $\eta_p^2 = 0.47$ . In addition, a significant interaction between Search Type and Task was obtained, F(1,15) = 16.09, p = .001,  $\eta_p^2 = 0.52$ , due to a greater difference in error rates between tasks in retroactive search compared to perceptual search trials (cf., Fig. 2). Post-hoc dependent *t*-tests revealed that the performance difference between tasks was significant in retroactive search trials, t (15) = 4.03, p = .002,  $g_{av} = 0.72$ , but not in perceptual search trials, t (15) = 1.25, p = .23,  $g_{av} = 0.16$ .

The analysis of RTs indicated slower responses in retroactive search trials (mean RT = 907.63 ms, SE = 127.75) compared to perceptual search trials (mean RT = 808.56 ms, SE = 95.94), F(1,15) = 6.12, p = .02,  $\eta_p^2 = 0.29$ , and in sound localization trials (mean RT = 850.63 ms, SE = 47.13) compared to sound detection trials (mean RT = 726.14 ms, SE = 43.95), F(1,15) = 23.51, p = .002,  $\eta_p^2 =$ 



Fig. 2. Mean proportion of erroneous trials (%) and reaction times (ms) dependent on task for perceptual (A) and retroactive search (B). Error bars indicate the standard error of the mean. Please note that the tasks included different numbers of response alternatives (i.e., two versus three response choices in sound detection and sound localization, respectively), leading to different levels of chance for sound detection (i.e., 50%) compared to sound localization (i.e., 33.3%).

0.61. The interaction of Search Type and Task did not reach statistical significance, F(1,15) = 2.92, p = .11,  $\eta_p^2 = 0.16$ .

#### 3.2. Oscillatory activity

In a first step, we assessed latency differences between perceptual and retroactive search. For stimulus-locked data, mid-point latencies in perceptual (FAL<sub>50</sub> = 583 ms post sound array) and retroactive search trials (FAL<sub>50</sub> = 694 ms post target sound) did not differ significantly, t (15) = -1.522, p = .15. Thus, to determine a time window for the subsequent analysis of alpha power amplitude, the FAL<sub>50</sub> was assessed in the grand average stimulus-locked ERSP, that is, the ERSP averaged across all conditions (FAL<sub>50</sub> = 640 ms). In contrast, in the responselocked data, alpha lateralization occurred significantly later for retroactive (FAL<sub>50</sub> = 90 ms post response) than for perceptual search trials (FAL<sub>50</sub> = 206 ms prior to response), as indicated by a significant difference in FAL<sub>50</sub>, t(15) = -2.94, p = .01.

Subsequently, the amplitude differences in posterior alpha power lateralization were investigated. In the stimulus-locked data, mean alpha power was measured in a time window ranging from 534 to 730 ms (relative to the second sound stimulus) in all conditions; that is, in a 200 ms-time window set around the grand average FAL<sub>50</sub> (see above). The analysis revealed a main effect of Search Type, F (1,15) = 10.95, p = .005,  $\eta_p^2 = 0.42$ , with an overall greater suppression of alpha power in retroactive search trials (Mean<sub>(retro)</sub> = -1.76 dB, SE = 0.29) compared to perceptual search trials (Mean<sub>(perc)</sub> = -1.23 dB,

SE = 0.32). This main effect is illustrated in Fig. 3, depicting the overall magnitude of power between 6 and 30 Hz depending on search type. In addition, a main effect of Asymmetry indicates the significant overall lateralization of alpha power, with greater alpha suppression contralateral (Mean<sub>(contra)</sub> = -1.66 dB, SE = 0.27, Mean<sub>(ipsi)</sub> = -1.33 dB, SE = 0.31) to the target sound, F(1,15) = 13.97, p = .002,  $\eta_p^2 = 0.48$ . Fig. 4 exemplarily contrasts the contralateral and ipsilateral portions of oscillatory power (6-30 Hz) at posterior electrodes PO7/8 and P7/8 for perceptual and retroactive search, respectively. As clearly evident by visual inspection (see Fig. 4A and C) the asymmetry appears to be restricted to sound localization (and absent in sound detection). A significant interaction of Task and Asymmetry confirms this observation, F  $(1,15) = 12.84, p = .003, \eta_p^2 = 0.46$ . Post-hoc dependent *t*-tests, contrasting the mean ipsilateral and contralateral alpha power in the sound localization condition, t(15) = -4.07, p = .002,  $g_{av} = 0.38$ , and the sound detection condition, t(15) = -0.38, p = .71,  $g_{av} = 0.03$ , corroborated this finding. Importantly, this interaction was independent from Search Type, F(1,15) = 0.85, p = .37,  $\eta_p^2 = 0.05$ .

To investigate the extent to which the observed alpha lateralization reflects response-related processes, the response-locked ERSPs were analyzed. The corresponding time-frequency plots and scalp topo-graphies are displayed in Fig. 4, section B and D. Here, the analysis revealed a highly similar pattern of results. Please note, however, that for the response-locked data, different 200 ms measurement windows were applied for perceptual (310–110 ms prior to response) and retro-active search trials (16 ms prior to and 184 ms after response), due to



**Fig. 3.** Stimulus-locked time frequency plots illustrating overall oscillatory power from 6 to 30 Hz averaged across the electrodes of interest, that is PO7/8, P7/8, P5/6, and TP7/8. The figure illustrates the main effect of search type with stronger alpha desynchronization in retroactive compared to perceptual search. The red rectangles highlight the time window used for statistical analyses. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article).



**Fig. 4.** Results for the perceptual (A/B) and retroactive (C/D) search conditions. (A) and (C) depict the stimulus-locked data, (B) and (C) the response-locked data. The time frequency plots on the left-hand side of each section illustrate the contralateral and ipsilateral portions of power in a frequency range from 6 to 30 Hz at electrodes PO7/8 and P7/8 for perceptual and retroactive search, respectively, where the effect was most pronounced. White dots indicate the electrode cluster chosen for statistical analyses. Mean alpha power (8–12 Hz) was analyzed in a 200 ms time window highlighted by the red rectangles. On the right-hand side, the respective scalp topographies, based on a subtraction of contralateral minus ipsilateral alpha power, are depicted. Because the subtraction was mirrored across both hemispheres, the topographies are symmetrical. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article).

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**Fig. 5.** Bar graph, illustrating the contrast between contralateral and ipsilateral portions of alpha power (dB) dependent on task for both stimulus-locked (A) and response-locked (B) data. To illustrate the significant interaction of Task and Asymmetry (cf., plots at the far right-hand side), data were averaged across search types. Please note, there was no significant three-way interaction of Task, Asymmetry, and Search Type. Error bars indicate the standard error of the mean.

the significant latency difference described above. Here, the time windows indicate a 200 ms time period set around the FAL<sub>50</sub> measured in perceptual and retroactive search (see above). The analysis revealed a significant main effect of Asymmetry, F(1,15) = 6.80, p = .02,  $\eta_p^2 =$ 0.31, indicating a general lateralization of alpha power, with stronger alpha suppression contralateral (M = -1.44 dB, SE = 0.21) compared to ipsilateral (M = -1.24 dB, SE = 0.25) to the target sound. Consistent with the stimulus-locked data, a significant interaction of Task and Asymmetry indicates that the lateralization only occurred for sound localization, but not detection, F(1,15) = 7.80, p = .01,  $\eta_p^2 = 0.34$ . Post-hoc dependent t-tests confirmed a significant lateralization of alpha power in the sound localization, t(15) = -3.09, p = .014,  $g_{av} =$ 0.33, but not in the sound detection condition, t(15) = -0.009, p = .99,  $g_{av} = 0.0007$ . Again, analogous to the stimulus-locked results, the asymmetry occurred irrespective of search type, as indicated by a nonsignificant interaction of Task, Asymmetry, and Search Type, F (1,15) = 0.06, p = .80,  $\eta_p^2 = 0.004$ . Fig. 5 summarizes the results, contrasting the main findings of the stimulus- and response-locked analyses in a bar chart.

As mentioned above, we averaged the data across electrode sides to reduce the family-wise error rate. However, additional analyses including Electrode as a factor in the ANOVA yielded qualitatively comparable results. Importantly, no higher-order interaction including Asymmetry, Electrode, Task, and Cue reached significance (all p > .16, Greenhouse-Geisser corrected values,  $\eta_p^2 < 0.12$ ). Thus, we cannot prove that the observed scalp topographies (cf., Fig. 4) in perceptual and retroactive search differ significantly from each other.

In addition, to quantify the onset of the response-locked asymmetries, and thereby, to further test whether alpha lateralization in localization conditions was associated with response preparatory processes, we calculated the 20% fractional area latency (FAL<sub>20</sub>) in the respective

response-locked ERSPs [61]. That is, we assessed the point in time that divides the first 20% of the area under the difference curve from the last 80%. Using a jackknife approach, analogous to the  $FAL_{50}$ , the negative area under the difference curve was measured in a broad time window ranging from 500 ms before to 200 ms after the response. In both search conditions, the onset of the asymmetry was clearly before the response, with a  $FAL_{20}$  of 322 ms in perceptual and 152 ms in retroactive search trials, respectively.

#### 4. Discussion

A vast amount of studies has established the central role of alpha oscillations in the deployment of spatial attention in both perceptual and mnemonic space. However, with the majority of findings relating to visual processing, the importance of spatially-specific modulations of alpha power in auditory spatial attention, retroactive attention in particular, remains elusive. To address this gap, we investigated the role of posterior alpha lateralization in deploying attention within a sound array in external space (i.e., perceptual attention) as opposed to representations of a sound array held in working memory (i.e., retroactive attention). In both search conditions, participants completed a sound localization and a sound detection task block, enabling us to unravel the significance of alpha lateralization under task demands requiring a spatially-specific response in contrast to purely feature-based search. Here, we present evidence that auditory alpha lateralization operates in both external and internal space, suggesting a common neural attention mechanism for perceptual and retroactive shifts of spatial attention. Beyond that, we show that auditory alpha lateralization seems to be restricted to spatially-specific task demands, as it was not evident in purely feature-based search conditions.

In general, participants performed well on the task, with overall

faster response times and fewer errors for perceptual search compared to retroactive search, as well as for sound detection compared to sound localization. Considering that sound localization involves a higher computational effort [43], this difference between tasks seems intuitive. Regarding error rates, it was, however, only significant in retroactive search trials. The non-significant difference in error rates between tasks in perceptual search is most likely due to a ceiling effect. In addition, it should be noted that during sound localization blocks, participants chose from three response alternatives (i.e., left, right, or target absent), whereas sound detection required a choice from only two response alternatives (i.e., yes or no). This unbalance in response choices was introduced in order to control for strategy (cf., 2.3 Procedure and task). Hence, one may argue that reaction times and error rates may be partially influenced by the number of response alternatives in the respective tasks. However, if performance differences between sound localization and detection were solely based on differences in the number of response alternatives, the performance difference should be equally visible in retroactive and perceptual search.

Regarding the electrophysiological level, our findings provide new evidence for the claim that alpha power lateralization is not exclusively related to the deployment of visual spatial attention, but indeed extents to auditory spatial attention [32–34]. In particular, for the first time, we show that retroactive shifts of attention within an auditory working memory representation are reflected by a spatially-specific modulation of alpha power oscillations when participants were asked to indicate the spatial location of the target sound. Importantly, no such asymmetry was found when participants indicated the target's presence or absence.

The observed alpha asymmetries in perceptual and retroactive sound localization were strikingly similar, suggesting a common neural basis for external and internal shifts of attention. In addition, the presented scalp topographies appear highly comparable to alpha power modulations previously shown in visuo-spatial cueing paradigms [21,22,27,31] and retro-cueing studies [3,17,58], signifying an overlap of the involved mechanisms across domains. This corroborates the notion of a supramodal attention mechanisms that controls the deployment of attention irrespective of modality [63]. Yet, it needs to be kept in mind that no direct comparison between modalities was made in the current study.

Critically, the present study differs from most previous investigations of alpha power lateralization in that it used a central, non-spatial cue indicating the target's identity, instead of using a lateralized or spatial cue (e.g., an arrow). This results in several advantages: First, the use of a centrally presented non-lateralized cue in retroactive search allows to conclude that the alpha lateralization is genuinely based on an endogenous attentional mechanism, and not a shift of attention to the external hemifield indicated by an arrow [64]. Second, it enables us to unravel the role of spatially-specific attentional mechanisms under purely feature-based task demands. While there is a broad consensus on the involvement of alpha power in the spatially-specific deployment of attention, the question whether the selection of non-spatial features is similarly accomplished by a spatial attention mechanism continues to be a matter of debate. Hitherto existing evidence is limited to the visual domain and remains inconclusive [30,59,65,66]. For instance, a number of studies demonstrated non-lateralized modulations of alpha power in task-selective areas, such as modulations in color- and motionsensitive areas [30], or modulations in direction-sensitive occipital areas [66] when respective features were cued. While Wildegger et al. [65] found neither lateralized nor non-lateralized modulation of alpha power by additional target-identity information, van Diepen et al. [59] showed alpha lateralization in a non-cued task condition, though, only when the pre-defined target was paired with a low-similarity distractor (as opposed to a high-similarity distractor). In addition, a few visual retro-cueing studies, adopting a non-spatial color retro-cue, have provided evidence for the notion that the selection of a working memory representation based on feature information involves spatially specific

shifts of attention, as indicated by asymmetric ERP components [67] or posterior alpha lateralization [64]. These findings in favor of alpha power lateralization in non-spatial task settings are in line with the view that spatial position receives a "special status" in visual processing [68,69]; consequentially, making it inevitably a part of working memory representations. Corroborating this claim, in a visual working memory task, Foster et al. [70] recently demonstrated that alpha lateralization reflects the spontaneous encoding and maintenance of spatial positions in working memory, regardless of their task relevance. Using a decoding approach, Bae and Luck [71] showed that in a visual delayed estimation task, in which stimulus location provided no information about the task-relevant feature dimension orientation, alphaband oscillations carried precise information about the location of a stimulus, while object properties were decoded from phase-locked ERP voltage.

With spatial position being completely irrelevant to the task, these designs strongly resemble the retroactive sound detection paradigm presented here. Hence, the absence of alpha lateralization under nonspatial task demands in the present auditory search design, being inconsistent with these prior visual findings, may point towards fundamental differences between modalities regarding the involvement of alpha power in feature-based attention. Alternatively, Wildegger et al. [65] suggested that alpha power modulations may only support featurebased attention in tasks involving the gating of information processed by non-overlapping neural populations, such as color and motion [30,64] or relatively high-level feature representations. While this hypothesis could explain the lack of alpha lateralization in their study, using low-level feature information, it would imply to find an alpha lateralization with the rather complex, high-level animal vocalizations used here; thus, at least with respect to our auditory data, this explanation seems to not hold true.

With posterior alpha power lateralization being exclusively evident during spatially-specific task demands (i.e., sound localization) in the present study, it seems appealing to associate the observed asymmetry with a spatially-specific access to a supramodal template of the previously encoded information. Myers et al. [58] have previously proposed that alpha lateralization leads to a short-term spatiotopic increase in excitability for the cued item. That is, higher-order control areas might guide the access to the lower-level neural populations storing the to-be-retrieved information in visual cortex. We suppose that the latter is not restricted to visual information but might involve the access to supramodally stored contents. Presumably visual areas may be especially suited in this context, given that they provide an extremely high spatial resolution, due to direct projections of stimulus position, via the retina, to retinotopically organized visual cortex [72,73]. In other words, alpha lateralization might reflect the access to a supramodal response template, providing the spatially-specific information required to giving a spatially-specific response. Accordingly, the sound localization task seemed to involve access to a map of supramodal representations in space, while the sound detection task, only based on the selection of non-spatial features, did not. Concordantly, a closer observation of the time frequency plots in the localization condition (cf., Fig. 4) showed that the alpha lateralization seems to strongly coincide with the average response time. This proposed relation to response-related processes received further support from the responselocked analyses, showing a diminished but still clearly present lateralization of alpha power in both the perceptual and retroactive sound localization task, which was, again, absent in the sound detection conditions. Importantly, the onset of these response-locked asymmetries was clearly prior to the response, supporting the claim that it relates to the transfer of spatial information into a response-specific format.

The observed differences in alpha power modulations between sound localization and sound detection can be nicely aligned with the distinction of a "what" and "where" subsystem as proposed in the framework by Kubovy and van Valkenburg [74]. The authors highlight the indispensable role of pitch or frequency as primary stimulus attributes that constitute to the "what" dimension, that is, to auditory object formation. Critically, the latter is to be distinguished from vision, for which location presents the indispensable stimulus dimension. Empirical evidence brought forward by Maybery et al. [75] contributes to this framework, demonstrating that the primary feature (in their case the more global object identity in terms of verbal content) is encoded in an obligatory fashion, whereas spatial information as a secondary feature is only bound to verbal-identity when both features were task-relevant. Our study strengthens this proposal offering electrophysiological evidence in favor of a task-demand-related recruitment of (auditory or supramodal) spatial attention.

### 5. Conclusion

Taken together, what do the present results reveal about the involvement of spatially-specific attentive processing in sound localization and detection in perceptual and retroactive search? First, attentional deployment within external and internal auditory representations share overlapping neural mechanisms: That is, both search conditions revealed a lateralization of alpha power over posterior scalp sites in sound localization. The striking similarity to findings from the visual domain corroborates the notion of a higher-order supramodal attention mechanism that operates in perceptual and mnemonic space. The response-locked analyses suggest that alpha lateralization reflects a response-related process, providing a (potentially supramodal) spatial response template. Critically, we found no alpha asymmetry in purely feature-based sound detection trials, suggesting that auditory alpha lateralization is limited to task demands requiring a spatially-specific response.

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#### **Declarations of interest**

None.

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