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Dynamic alpha power modulations and slow negative potentials track natural shifts of spatio-temporal attention

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Abstract

Alpha power modulations and slow negative potentials have previously been associated with anticipatory processes in spatial and temporal top-down attention. In typical experimental designs, however, neural responses triggered by transient stimulus onsets can interfere with attention-driven activity patterns and our interpretation of such. Here, we investigated these signatures of spatio-temporal attention in a dynamic paradigm free from potentially confounding stimulus-driven activity using electroencephalography. Participants attended the cued side of a bilateral stimulus rotation and mentally counted how often one of two remembered sample orientations (i.e., the target) was displayed while ignoring the uncued side and non-target orientation. Afterwards, participants performed a delayed match-to-sample task, in which they indicated if the orientation of a probe stimulus matched the corresponding sample orientation (previously target or non-target). We observed dynamic alpha power reductions and slow negative waves around task-relevant points in space and time (i.e., onset of the target orientation in the cued hemifield) over posterior electrodes contralateral to the locus of attention. In contrast to static alpha power lateralization, these dynamic signatures correlated with subsequent memory performance (primarily detriments for matching probes of the non-target orientation), suggesting a preferential allocation of attention to task-relevant locations and time points at the expense of reduced resources and impaired performance for information outside the current focus of attention. Our findings suggest that humans can naturally and dynamically focus their attention at relevant points in space and time and that such spatio-temporal attention shifts can be reflected by dynamic alpha power modulations and slow negative potentials.

KEYWORDS
alpha power, EEG, slow negative potentials, spatial attention, temporal attention

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1 | INTRODUCTION

In a world with an ever-increasing amount of information permanently competing for access to severely limited human processing systems, top-down predictions of future events can help allocating attentional resources more efficiently. Covert shifts of attention (i.e., changes of mental focus in the absence of ocular movement) toward the *location* of expected, task-relevant events are known to bias performance and neural processing in favor of stimuli occurring at the locus of attention at the cost of stimuli occurring elsewhere (Di Russo et al., 2003; Foster et al., 2017; Luck et al., 2000; Posner, 1980; Samaha et al., 2016; Sauseng et al., 2005; Woldorff et al., 2002). But also expectations about the *onset* of an upcoming event have been found to boost behavioral and neural responses by dynamically guiding attention to relevant moments in time (Correa et al., 2006; Griffin et al., 2001; Lange & Röder, 2006; Nobre, 2001; Nobre et al., 2007; Nobre & van Ede, 2018).

Alpha oscillations, rhythmical brain activity around 10 Hz, are one of the most prominent electrophysiological signatures of visuospatial attention (Peylo et al., 2021). Covertly shifting the attentional focus to one part of the visual field in preparation of an upcoming, task-relevant event is typically associated with sustained alpha power desynchronization in posterior cortices contralateral to the locus of attention (Barne et al., 2020; Popov et al., 2019; Sauseng et al., 2005; Yamagishi et al., 2005) and occasional alpha power synchronization ipsilateral to it (Kelly et al., 2006; Rihs et al., 2007; Worden et al., 2000). In this context, a decrease in alpha power is thought to reflect cortical activation associated with increased neuronal excitability and facilitated information processing, whereas an increase in alpha power is interpreted as cortical deactivation associated with decreased neuronal excitability and inhibited information processing (Foxe & Snyder, 2011; Jensen & Mazaheri, 2010; Klimesch et al., 2007; Romei, Brodbeck, et al., 2008; Romei, Rihs, et al., 2008; Sauseng et al., 2009).

In line with this interpretation, posterior alpha power has successfully been used to classify the locus and time course of spatial attention (Foster et al., 2017; Samaha et al., 2016); and low pre-stimulus alpha activity and strong, attention-related alpha power asymmetry have been associated with improved visual performance and increased event-related potentials (ERPs; Ergenoglu et al., 2004; Hanslmayr et al., 2005; Hanslmayr et al., 2007; Thut et al., 2006; van Dijk et al., 2008). Moreover, non-invasive alpha power entrainment in one hemisphere has been found to improve visual perception for the ipsilateral hemifield and to impair performance contralaterally

(Kasten et al., 2020; Romei et al., 2010; Schuhmann et al., 2019; Taylor & Thut, 2012), providing evidence for a causal role of posterior alpha power in spatial, top-down attention (Peylo et al., 2021).

In addition to the strong support for the role of sustained alpha power (de-)synchronization in visuospatial attention, some studies suggest that posterior alpha power can also be transiently modulated through the attentional prioritization of relevant moments in time. Temporal expectations about the onset of an upcoming stimulus derived from the rhythmicity of a preceding stimulus sequence have been found to elicit posterior alpha power desynchronization around the anticipated target onset (Praamstra et al., 2006), which was associated with speeded stimulus discrimination and increased ERP amplitudes thereafter (Rohenkohl & Nobre, 2011). In line with this observation, aging-related impairments in the ability to allocate attentional resources to relevant moments in time have been associated with a reduction in anticipatory alpha power desynchronization (Zanto et al., 2011), suggesting that alpha power modulations might not only support spatial but also temporal top-down attention. In line with this interpretation, alpha power changes have been associated with both spatial and temporal orienting in combined spatio-temporal attention tasks (Heideman et al., 2018; van Ede et al., 2020).

Despite the evidence for alpha power modulations underlying both spatial and temporal shifts of attention, most classical experimental paradigms trigger one important component that might interfere with attention-driven alpha power changes and our interpretation of such, namely externally driven neural activity: The onset of a stimulus (such as a cue that is regularly being used to direct the participant's attention to the location of an upcoming target stimulus) and the sensory processing and cortical activation associated with it are typically accompanied by an evoked component and a desynchronization in the alpha frequency band. These externally triggered neural responses can then interfere with internally driven alpha power modulations in preparation of the imperative stimulus by either overwriting early attention-related alpha power desynchronization (in the case of stimulus-evoked activity) or by contaminating such while at the same time counteracting potential suppression-related alpha power synchronization (in the case of stimulus-related alpha power decreases). This issue becomes particularly problematic when considering temporal attention tasks, in which the temporal precision of attention-driven alpha power changes becomes even more crucial (a problem that is further intensified by the temporal smearing associated with typical filtering techniques) and where the alpha power modulations around task-relevant moments in time might not only be weaker than the effects associated with

spatial attention shifts (Meehan et al., 2021) but also regularly coincide with the onset of the anticipated stimulus.

These potential confounds have already been acknowledged in the past (Kelly et al., 2006; Praamstra et al., 2006; Rohenkohl & Nobre, 2011; Thut et al., 2006; Worden et al., 2000) and have been tried to be accounted for by the spatial attention community using lengthened cue-time intervals (increasing the distance between externally triggered neural responses and internally driven alpha power modulations), cross-modal cueing (segregating cue-processing brain areas from attention-guiding ones), or trial-overarching stimulus presentations (equating stimulus-driven activity before and after the attention-directing cue). In temporal attention tasks, anticipated target stimuli have further been occluded or entirely omitted (preventing externally triggered neural responses from the target itself but not necessarily from the rhythmic, prediction-inducing pre-stimuli). Despite the validity of these approaches, the most straightforward solution to this issue, which might help to uncover subtle, previously potentially masked alpha power dynamics and thereby elucidate the role of alpha oscillations in spatio-temporal attention, might be to prevent sharp stimulus onsets and the associated externally triggered neural responses in the first place. One possibility to achieve this goal could be to use a continuous stimulus presentation instead of discrete stimulus onsets, which allows participants to anticipate task-relevant events and to dynamically and naturally direct their attention accordingly.

In line with this consideration, here we used electroencephalography (EEG) to investigate alpha power modulations during simultaneous shifts of top-down attention in space and time, while participants performed a dynamic target detection task, free from potentially confounding stimulus-driven neural responses and alpha power modulations. In this task, participants attended the cued side of a continuous, bilateral stimulus rotation and mentally counted how often one of two remembered orientations (i.e., the target) was displayed, while ignoring the uncued side and non-target orientation. Based on the behavioral evidence for a potentiation of visuospatial attention benefits through temporal expectations (Doherty et al., 2005; Rohenkohl et al., 2014), we hypothesized that participants would naturally (i.e., without explicit instructions or cueing) and dynamically guide attention toward task-relevant moments in time (i.e., onset of the target orientation) at task-relevant locations in space (i.e., in the cued hemifield) at the expense of task-irrelevant locations and time points (i.e., the uncued hemifield and non-target orientation); and that such spatio-temporal attention shifts would be reflected by dynamic alpha power desynchronization over posterior electrodes contralateral to the locus

of attention (and potentially alpha power synchronization ipsilateral to it).

A second electrophysiological signature of temporal expectancies, which has previously been found to accompany anticipatory alpha power desynchronization (Praamstra et al., 2006; Sauseng et al., 2005; Worden et al., 2000; Zanto et al., 2011), is a slow negative deflection over task-relevant cortices. Such negative potentials have consistently been found to increase toward and then peak around task-relevant moments in time before returning back to baseline (Correa et al., 2006; Kononowicz & Penney, 2016; Miniussi et al., 1999). Their functional role, however, remains a matter of debate. Whereas temporal orienting and the associated slow negative potentials in anticipation of task-relevant events have traditionally been associated with preparatory processes primarily on the level of response decision and execution (Griffin et al., 2001, 2002; Miniussi et al., 1999; Nobre, 2001), more recent studies suggest that anticipatory benefits through temporal foreknowledge can already start on the perceptual level (Correa et al., 2005, 2006; Mathewson et al., 2010; Rohenkohl et al., 2012; Vangkilde et al., 2012) and that slow negative waves might constitute a signature of such sensory preparation (Bianco et al., 2020; Di Russo et al., 2019). Stimulus–response contingencies in typical attention tasks, however, can hinder a successful dissociation between perceptual and motor-related preparatory processes. Only recently, using simultaneous manipulations of stimulus–response compatibilities and visuospatial attention researchers were able to demonstrate a response-independent increase in anticipatory negative potentials toward target onset over posterior electrodes contralateral to the locus of attention, which was associated with improved performance thereafter (Di Russo et al., 2021), supporting a functional role of slow negative potentials for the attention-driven tuning of perception toward task-relevant moments in time.

In the present study, we took advantage of our dynamic target detection task, which was designed to minimize decision- and motor-related processes by neither requiring overt responses nor enabling response decisions until the end of the rotation, to further investigate the perceptual account and dynamic nature of anticipatory negative potentials. We hypothesized that, if temporal attention and the associated negative slow waves are indeed related to preparatory processes on the perceptual level, we should observe a dynamically increasing negativity toward the anticipated, task-relevant moments in time (i.e., onset of the target orientation) at task-relevant locations in space (i.e., in the cued hemifield) over electrodes contralateral to the locus of attention, similar to the predictions for anticipatory alpha power reductions.

2 | METHOD

2.1 | Participants

Thirty-two volunteers recruited at the Ludwig Maximilians University, Germany, participated in the experiment in exchange of financial compensation or lab tokens after having given written informed consent. Three participants did not fulfill the minimum performance criterion in either of the two tasks described below (counting performance <50% and/or matching performance <60%) and were excluded from all following analyses. The final sample consisted of 29 participants (20 female, 9 male; 27 right-handed, 2 left-handed according to the Edinburgh Handedness Inventory; Oldfield, [1971](#)) and had a mean age of 23.62 years (SD = 4.17). All participants reported normal or corrected-to-normal vision and no history of neurological or psychiatric disorders. The study was approved by the local ethics committee and was conducted in accordance with the Declaration of Helsinki.

2.2 | Experimental design

In the present experiment, we recorded EEG (see Section [2.3](#)) while participants performed two parallel tasks. In the first part of each trial, participants performed a dynamic target detection task (*counting task*), in which they were asked to focus their attention on the cued side of the screen and mentally count how often the orientation of a continuously rotating stimulus matched the orientation of one of two previously presented, to-be-remembered sample stimuli (i.e., the target) while ignoring the uncued side and non-target orientation. In the second part of each trial, participants performed an event-related *delayed match-to-sample task*, in which they were asked to indicate if the orientation of a probe stimulus matched the orientation of the corresponding sample stimulus or not (see [Figure 1](#); for a clip of the paradigm visit https://osf.io/dre2c/).

Stimuli in both tasks were controlled using Presentation 20.1 (Neurobehavioral Systems®) and were displayed on a central 17-inch Acer V176 monitor (1280 × 1024 resolution, 60 Hz refresh rate) placed in a dimly lit room. At the beginning of the experiment, participants were seated in a comfortable chair with a standard keyboard placed on their lap and were asked to place their right index, middle, and ring finger on the keys "1", "2" and "3" of the keyboard's number pad (counting response) and their left middle and index finger on the keys "S" (same) and "D" (different; matching response), respectively.

Each trial started with the presentation of two differently oriented but otherwise identical multi-colored ring stimuli (1000 ms each, ca. 6.1° × 6.1° visual angle, with detailed and homogeneously distributed color and texture information to allow for sufficient visual orientation discrimination while also encouraging participants to remember the entire stimulus instead of focusing on just one prominent feature), which were displayed one after another on opposite sides of a gray screen (50% left–right vs. 50% right–left). Participants were instructed to remember the orientation of both sample stimuli as precisely as possible while maintaining fixation at the central white cross hairs (ca. 0.8° × 0.8° visual angle), which were visible throughout the experiment to help participants stabilize their gaze during the lateralized stimulus presentation. After a delay of 500 ms, a retro-cue was presented in the shape of a central, yellow arrow (300 ms, ca. 1.9° × 0.6° visual angle), pointing to either side of the screen (50% left vs. 50% right) to indicate which of the previously presented orientations and which side of the screen were to be attended (and which to be ignored) during the following counting task.

Immediately after cue offset, both ring stimuli reappeared in a new pseudo-random orientation. Starting from this position, both rings began to rotate in the same direction (randomly clockwise or anti-clockwise, but never in the same direction for more than two successive trials to minimize potential motion after-effects) and with constant but different speeds (randomly with 90°/sec and 150°/sec or 120°/sec and 180°/sec). During the rotation (lasting between 5333 ms and 6933 ms), participants were instructed to covertly attend the previously cued side of the screen and to count as precisely as possible how often (one, two, or three times) the target orientation was adopted, while ignoring the uncued side and non-target orientation. Due to the steady stimulus rotation, participants were able to predict when these task-relevant events were about to happen (similar to a clock foretelling the upcoming hour), allowing them to focus their attention on task-relevant points in space and time accordingly and thereby facilitate perceptually demanding discriminations between target and stimulus orientations (e.g., when the stimulus rotation approaches the target orientation but stops shortly beforehand). At the end of the rotation, participants were asked to provide their answer by pressing the corresponding number on the keyboard, which terminated the counting task and the first part of the trial.

Following the response and a short break of 100 ms, the delayed match-to-sample task in the second part of the trial was initiated. In this task, a single ring stimulus (1000 ms) was displayed on either side of the screen (50% left vs. 50% right) with its orientation either matching or mismatching (50% match vs. 50% mismatch; mismatch by +/− 10°/20°/30°/40°/50°/60° with equal probability) the orientation of the probed sample stimulus previously
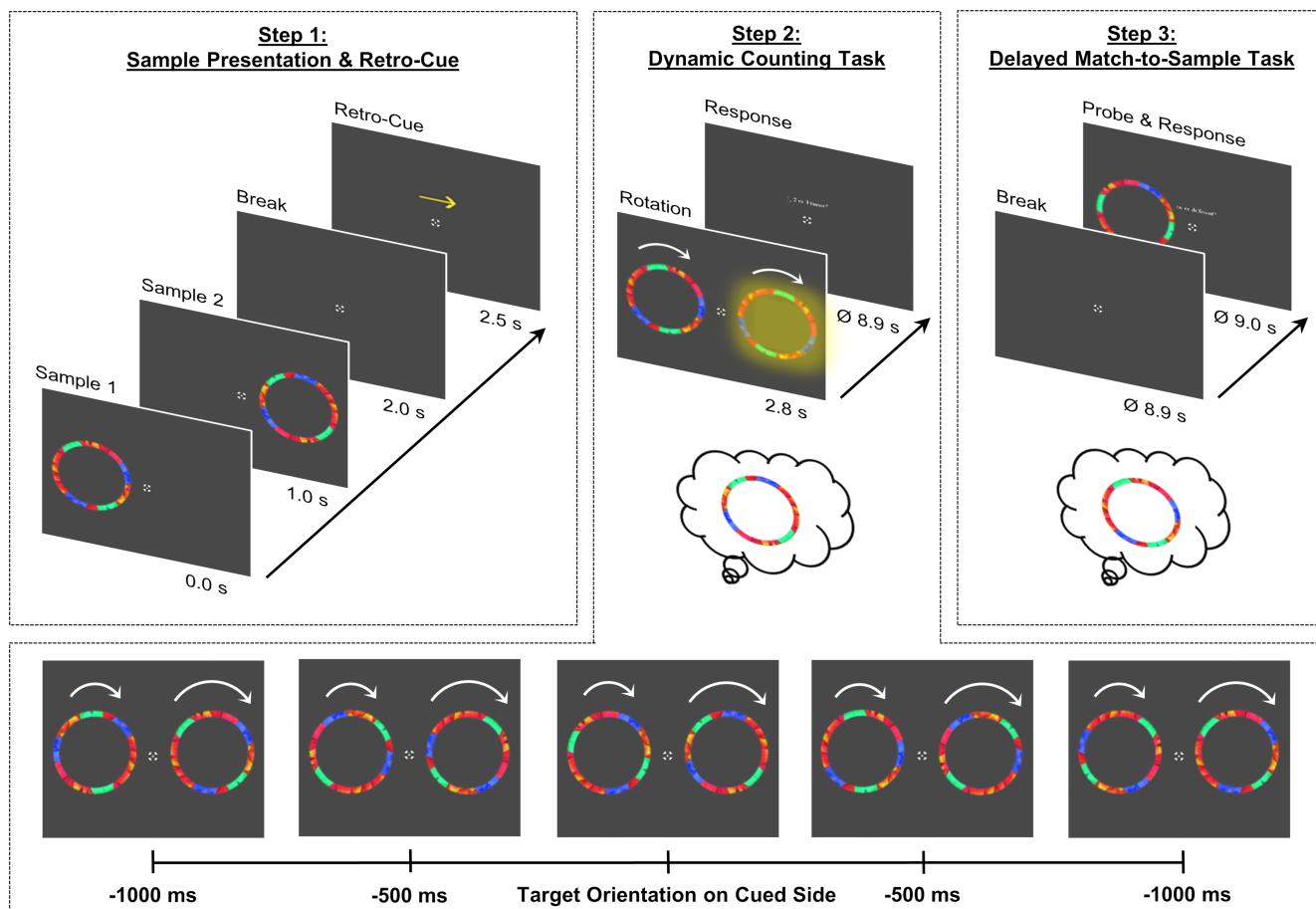
FIGURE 1 Example trial of the dynamic target detection task (counting task) and the event-related delayed match-to-sample task. Each trial started with the presentation of two differently oriented, to-be-remembered sample stimuli followed by a retro-cue (arrow pointing to the left or right), indicating which of the previously presented sample orientations and which side of the screen were to be attended during the following stimulus rotation (yellow gleam indicates which hemifield the participant would attend; note, the gleam was not shown in the experiment). The bottom row highlights the events taking place during the stimulus rotation (i.e., both rings rotating in the same direction with different speeds indicated by the arrows of different length) and the corresponding analysis window centered around the time points of interest (e.g., target orientation on the cued side of the screen). Participants were asked to count how often the target orientation (i.e., the one that they were cued to remember) was shown on the cued side of the screen, while ignoring the non-target orientation (i.e., the one that they were not cued to remember) and the uncued side of the screen. At the end of the rotation, participants registered their response to the counting task by button press. Afterwards, participants were presented with a probe stimulus and were asked to indicate if its orientation matched the orientation of the sample stimulus previously presented on the same side of the screen or not, independent of whether this sample had previously been the target or non-target. Stimuli in this figure have been increased in size and contrast for illustration purposes.

presented on the same side of the screen (50% target vs. 50% non-target). Participants were asked to judge as accurately as possible if the probe's orientation matched the orientation of the corresponding sample stimulus or not (irrespective of whether it had previously been the target or non-target). The delayed match-to-sample task therefore required participants to remember not only the counting-relevant target orientation throughout the stimulus rotation but also the counting-irrelevant non-target orientation, which could have otherwise been forgotten after presentation of the post-cue. This enabled us to investigate not only the predicted dynamic alpha power decreases related to the prioritization of task-relevant information (i.e., onset of the target orientation), but also potential dynamic alpha power increases related to the suppression of task-irrelevant and possibly interfering information (i.e., onset of the non-target orientation). Participants registered their response by pressing the corresponding button on the keyboard, which terminated the trial (500 ms inter-trial interval with 10% jitter). In total, the paradigm included three training blocks of 10 trials with feedback (partial or total repetition upon request) and four test blocks of 48 trials without feedback (one of four equiprobable randomization versions) and took approximately 60 min adding up to a total experiment duration of about 2 h including EEG preparation and breaks.

2.3 | EEG recording and preprocessing

Throughout the experiment, EEG was recorded from 62 scalp locations using passive Ag/AgCl electrodes mounted in an elastic cap (Easycap, Brain Products®), which was positioned in accordance with the extended 10–10 system. An electrode on the tip of the nose was used as reference and electrode position FPz served as ground. To correct for ocular artifacts later on, vertical and horizontal eye movements were recorded with two additional electrodes placed above the left eye and next to its outer canthus, respectively. Electrode signals between 0.016 and 250 Hz were digitized using a BrainAmp DC amplifier (1000 Hz sampling rate, 0.1 μV resolution, Brain Products®) and recorded using BrainVision Recorder 2.0.5 (Brain Products®). Electrode impedances were held below 10 kΩ throughout the recording.

EEG data were later offline preprocessed using BrainVision Analyzer 2.1.2 (Brain Products®). First, raw EEG data were filtered using a high- and low-pass filter (zero phase shift Butterworth filters with a slope of 48 dB/oct) with a cutoff at 0.1 and 100 Hz, respectively, and electrical line noise was removed using a 50 Hz Notch filter (with a slope of 96 dB/oct and a bandwidth of 5 Hz). Afterwards, noisy and slow-drift channels were visually identified and replaced using topographic interpolation by fourth-order spherical splines in affected blocks. EEG channels were then re-referenced using a common average reference, and large artifacts were visually identified and excluded from further processing. In the following semi-automatic (ocular correction) Independent Component Analysis (ICA), artifacts caused by eye movements and other systematic sources of interference, as well as channel-specific noise were removed. Lastly, small artifacts remaining after the ICA were visually identified and excluded from all following EEG analyses.

2.4 | Behavioral analyses

Performance in the dynamic counting task and the delayed match-to-sample task was quantified using response accuracy and speed (despite both tasks being non-speeded to rule out potential condition differences caused by different speed-accuracy trade-offs). Trials were considered correct if participants provided a single, valid response and the corresponding reaction times were logarithmized to account for their typical right-skewed distribution and summarized by computing the median for each participant separately. Performance (accuracy/speed) in the delayed match-to-sample task was computed for each probe identity (target/non-target) and orientation

(0°/10°–20°/30°–40°/50°–60°) separately; data were then analyzed using two-way repeated measures ANOVAs with Greenhouse–Geisser correction applied where necessary. The following post-hoc tests (0° vs. 10°–20°/30°–40°/50°–60°, 10°–20° vs. 30°–40° vs. 50°–60°) were carried out using Bonferroni-corrected, paired t tests. Accuracy in the counting task and the delayed match-to-sample task was correlated using a one-tailed Spearman rank correlation and its Bayesian equivalent using the method suggested by van Doorn et al. (2020).

All computations and statistical analyses were carried out in the Spyder 4.1.5 environment (Spyder Developer Team, 2020) for Python 3.7.3 (Van Rossum & Drake, 2009) using custom-written scripts and various open-source packages (EasyGUI 0.98.1, EasyGui Developer Team, 2017; matplotlib 3.3.2, Hunter, 2007; more-itertools 8.5.0, More-itertools Developer Team, 2020; NumPy 1.19.2, Harris et al., 2020; pandas 1.1.3, McKinney, 2010; pingouin 0.2.7, Vallat, 2018; prettytable 0.7.2, Prettytable Developer Team, 2013; rpy2 3.5.1, Rpy2 Developer Team, 2022; SciPy 1.5.4, Virtanen et al., 2020; seaborn, Waskom, 2021; termcolor 1.1.0, Termcolor Developer Team, 2011).

2.5 | EEG analyses

All EEG analyses were carried out using custom-written Python scripts and the MNE-Python 0.21.0 package (Gramfort et al., 2013). First, preprocessed EEG data from the 62 scalp locations during the stimulus rotation of the dynamic counting task were segmented into epochs from −1000 to +1000 ms around all stimulus orientations of interest (target/non-target orientation on the cued/uncued-left/right side of the screen). Afterwards, epochs with artifacts, incorrect counting responses, and/or saccades in the time window of interest (from −500 to +500 ms around orientation onset) were removed. Differences between the resulting number of available epochs per condition were eliminated using pseudo-random epoch sub-sampling (minimizing timing differences between conditions). On average, 101.00 ($SD = 24.40$) segments remained in each condition for the following analyses.

For alpha power analyses, the resulting epochs of each condition were transformed into time-frequency representations using 5-cycle Complex Morlet Wavelet analyses. To test if the predicted power effects were specific to the hypothesized alpha frequency range (8–12 Hz), time-frequency decompositions were performed for an extended frequency range from 5 to 15 Hz. The resulting power values were averaged across epochs and cropped to the time window of interest (from −500 to +500 ms around the stimulus orientation of interest), cutting off any data potentially affected by edge artifacts (Cohen, 2014). For

the analysis of static alpha power modulations, the resulting power values were baseline-corrected by subtracting the mean power from the 500-ms inter-trial interval (i.e., power averaged across clean and saccade-free epochs from −3000 to −2500 ms before cue onset). Afterwards, the baseline-corrected power values were combined into two spatial attention conditions (attention left: target/non-target orientation on the cued-left or uncued-right side of the screen; attention right: target/non-target orientation on the cued-right or uncued-left side of the screen) and averaged across the time window of interest (from −500 to +500 ms around the stimulus orientation of interest) to yield an estimate of static alpha power modulations following spatial attention shifts. Static power changes were statistically compared between the two spatial attention conditions (attention left vs. attention right) using a two-tailed, spatio-spectral cluster-based permutation test (based on the cluster sum of channel-frequency-wise t-values with 1024 permutations and an initial p-value of $p = .05$; Maris & Oostenveld, 2007). For the analysis of dynamic alpha power modulations, power values were baseline-corrected using a z-transformation across the full time window (from −500 to +500 ms around orientation onset) to reveal orientation-dependent power fluctuations over time (similar to Klimesch et al., 1998; Zanto et al., 2011). Dynamic power modulations were statistically tested for each condition separately (target/non-target orientation on the cued/uncued-left/right side of the screen to account for the bidirectional nature of alpha oscillations with power decreases contralateral to the locus of attention and/or power increases ipsilateral to it and the importance of distinguishing between these two functionally distinct alpha signatures) using one-tailed, spatio-spectral-temporal cluster-based permutation testing (based on the cluster sum of channel-frequency-time-wise t-values from −500 to +500 ms around the stimulus orientation of interest with 1024 permutations and an initial p-value of $p = .001$ to account for increased cluster extents in 3D space; Maris & Oostenveld, 2007).

For ERP analyses, epochs of each condition were averaged into eight separate ERP traces (target/non-target orientation on the cued/uncued-left/right side of the screen), which were later baseline-corrected (using the first 200 ms as baseline) and smoothed (using a 0.1–30 Hz band-pass FIR filter with Hamming window). Afterwards, ERPs were combined into *Left–Right* difference waves and statistically compared at each channel and time point using a mass-univariate, repeated-measures ANOVA with factors *Orientation* (target/non-target) and *Side* (cued/uncued) to test our hypothesis of increased slow wave negativity around task-relevant points in space and time (i.e., onset of the target orientation on the cued side of the screen). Multiple comparison correction was performed using

spatio-temporal cluster-based permutation testing (based on the cluster sum of channel-time-wise F-values from −1000 to +1000 ms around the stimulus orientation of interest with 1024 permutations and an initial p-value of $p = .01$ to account for moderate cluster extents in 2D space; Maris & Oostenveld, 2007).

To test the functional relevance of any observed power and/or ERP effects (see Sections 3.2–3.4), we computed each participant's individual EEG signature (i.e., the difference between the two clusters' mean power difference for static alpha power analyses, the mean cluster power for dynamic alpha power analyses and the mean *Orientation-by-Side* interaction for difference ERP analyses) and correlated those with performance in the dynamic counting task and the delayed match-to-sample task. Depending on the presence of outliers, we computed either Pearson's correlation coefficient (i.e., for the relationship between EEG parameters and target/non-target/non-target-mismatch probe accuracy in the delayed match-to-sample task) or Spearman's rank correlation (i.e., for the relationship between EEG parameters and overall accuracy in the counting task and the delayed match-to-sample task, as well as for non-target-match probe accuracy), which were tested against zero using one-tailed t-tests (with the assumption that static alpha power lateralization as well as dynamic alpha power desynchronization and ERP negativity around onset of the target orientation on the cued side of the screen would be beneficial to performance). In addition to these frequentist correlation analyses, we also computed Bayesian correlation tests (again using either Pearson's or Spearman's correlation coefficient depending on the presence of outliers; the former using pre-implemented functions and the latter using the ones suggested by van Doorn et al., 2020) to provide additional evidence for the observed relationships (e.g., a true null correlation, BF_{01}, or a true positive correlation, BF_{10}^{+}).

In a last step, we tested whether the observed effects of dynamic alpha power and slow negative potentials constituted two individual signatures of spatio-temporal attention shifts or whether they simply reflected one and the same underlying mechanism expressing itself in different aspects of the data (frequency vs. time). To this aim, we correlated the previously computed cluster means for dynamic alpha power modulations and ERP *Orientation-by-Side* interactions using a two-tailed Pearson correlation and its Bayesian equivalent. If the observed slow negative potential was simply a reflection of the corresponding alpha power modulation in the time domain or vice versa, then those participants showing strong effects of slow wave negativity should also be the ones to exhibit strong effects of alpha power. If, however, slow negative potentials and dynamic alpha power represented two independent signatures of spatio-temporal attention, then

we would expect no substantial correlation between the two effects.

3 | RESULTS

3.1 | Behavior

Participants performed well in both tasks with a small numerical advantage of the dynamic counting task (accuracy: $M = 81.25\%$, $SE = 2.10\%$; reaction times: $M_{log} = 6.63$ corresponding to a mean reaction time of 757.48 ms, $SE_{log} = 0.06$) over the event-related delayed match-to-sample task (accuracy: $M = 71.37\%$, $SE = 1.18\%$; reaction times: $M_{log} = 7.32$ corresponding to a mean reaction time of 1510.20 ms, $SE_{log} = 0.05$; see Figure 2). Accuracy in the counting task was further significantly and positively correlated with

accuracy in the subsequent matching task ($r(27) = .55$, $p < .001$, $BF_{10}^+ = 48.74$). Accuracy in the delayed match-to-sample task was also significantly higher for probes of the target orientation ($M = 70.55\%$, $SE = 1.26\%$) than for probes of the non-target orientation ($M = 65.05\%$, $SE = 2.02\%$; $F(1, 28) = 8.97$, $p = .006$, $\eta_p^2 = .243$). Additionally to probe identity, matching accuracy was significantly affected by probe orientation ($F(3, 84) = 88.93$, $p < .001$, $\eta_p^2 = .761$): Accuracy was significantly higher for matching probes (0°: $M = 78.52\%$, $SE = 2.14\%$) compared to mismatching probes (10°–20°/30°–40°/50°–60°: $M = 64.22\%$, $SE = 2.02\%$; $t(28) = 4.18$, $p = .001$, $\eta^2 = .290$) and for large mismatch degrees (50°–60°: $M = 86.75\%$, $SE = 1.84\%$) compared to moderate mismatch degrees (30°–40°: $M = 67.57\%$, $SE = 2.90\%$; Large–Moderate: $t(28) = 8.96$, $p < .001$, $\eta^2 = .361$) and small mismatch degrees (10°–20°: $M = 38.36\%$, $SE = 2.60\%$; *Moderate–Small*: $t(28) = 10.67$, $p < .001$, $\eta^2 = .494$). This increase in accuracy
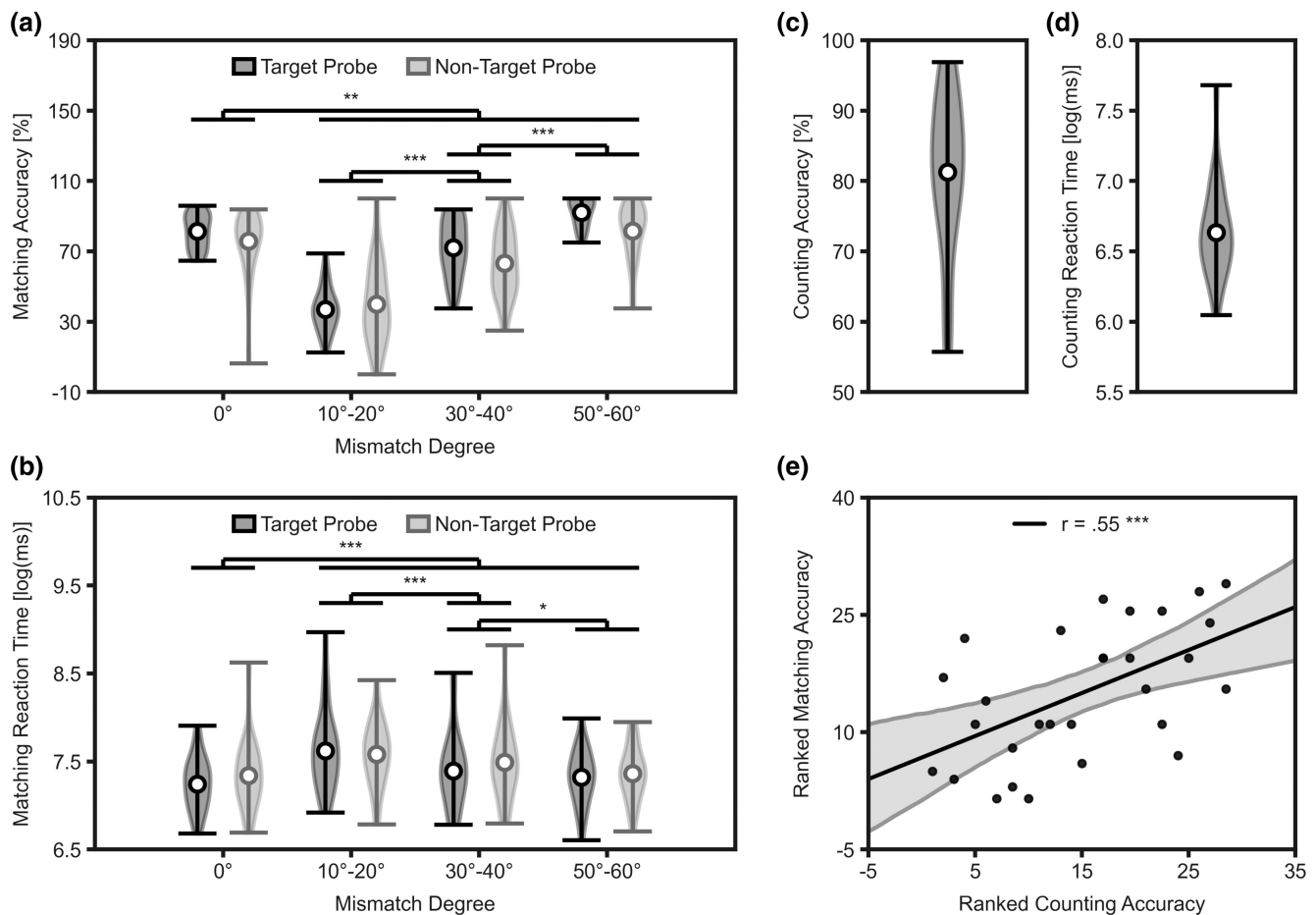

FIGURE 2 Performance in the dynamic counting task and the delayed match-to-sample task (a) Accuracy in the delayed match-to-sample task was improved for probes of the target compared to the non-target orientation and for matching compared to mismatching probes (with an increasing advantage for decreasing mismatch degrees) (b) Reaction times in the delayed match-to-sample task showed the same benefit for matching compared to mismatching probes and for larger compared to smaller mismatch degrees (c and d) Performance (accuracy/speed) in the dynamic counting task was slightly better than in the delayed match-to-sample task (e) The correlation between the ranked accuracy in both tasks shows that participants who performed well in the dynamic counting task also performed relatively better in the following delayed match-to-sample task. Dots represent means across the sampling distribution illustrated by violin plots and shaded areas denote 95% confidence intervals. Asterisks indicate statistical significance, where * $\triangleq$ $p < .05$, ** $\triangleq$ $p < .01$ and *** $\triangleq$ $p < .001$.

with increasing mismatch degree was by trend more pronounced for probes of the target orientation (10°–20°: $M = 36.85\%$, $SE = 2.35\%$, 30°–40°: $M = 71.98\%$, $SE = 3.07\%$, 50°–60°: $M = 92.03\%$, $SE = 1.52\%$) than for probes of the non-target orientation (10°–20°: $M = 39.87\%$, $SE = 4.21\%$, 30°–40°: $M = 63.15\%$, $SE = 3.50\%$, 50°–60°: $M = 81.47\%$, $SE = 2.97\%$; $F(3, 84) = 3.05$, $p = .060$, $\eta_p^2 = .098$).

Similarly, reaction times in the delayed match-to-sample task were significantly affected by probe orientation ($F(3, 84) = 25.55$, $p < .001$, $\eta_p^2 = .477$): Reaction times were significantly shorter for matching probes (0°: $M_{log} = 7.29$ corresponding to a mean reaction time of 1465.57 ms, $SE_{log} = 0.06$) compared to mismatching probes (10°–20°/30°–40°/50°–60°: $M_{log} = 7.46$ corresponding to a mean reaction time of 1737.15 ms, $SE_{log} = 0.06$; $t(28) = -4.99$, $p < .001$, $\eta^2 = .067$) and for large mismatch degrees (50°–60°: $M_{log} = 7.34$ corresponding to a mean reaction time of 1540.71 ms, $SE_{log} = 0.05$) compared to moderate mismatch degrees (30°–40°: $M_{log} = 7.44$ corresponding to a mean reaction time of 1702.75 ms, $SE_{log} = 0.07$; *Large–Moderate*: $t(28) = -2.93$, $p = .027$, $\eta^2 = .021$) and small mismatch degrees (10°–20°: $M_{log} = 7.60$ corresponding to a mean reaction time of 1998.20 ms, $SE_{log} = 0.07$; *Moderate–Small*: $t(28) = -4.21$, $p < .001$, $\eta^2 = .042$). This decrease in reaction time with increasing mismatch degree was independent of probe identity ($F(3, 84) = 1.59$, $p = .207$, $\eta_p^2 = .054$), as were overall reaction times (*Target*: $M_{log} = 7.39$ corresponding to a mean reaction time of 1619.71 ms, $SE_{log} = 0.06$ vs. *Non-Target*: $M_{log} = 7.44$ corresponding to a mean reaction time of 1702.75 ms, $SE_{log} = 0.06$; $F(1, 28) = 1.88$, $p = .182$, $\eta_p^2 = .063$).

3.2 | Static alpha power

Our static alpha power analysis revealed two posterior electrode clusters, a left-hemispheric one (centered around electrode P3) and a matching right-hemispheric one (centered around electrode P4), whose spectral power was significantly affected by the spatial allocation of attention throughout the rotation of the dynamic counting task: In both clusters, a broad range of frequencies (from around 5 to 15 Hz with a peak in the 8–12 Hz alpha frequency range) showed a power reduction during the stimulus rotation relative to the inter-trial baseline and this power decrease was significantly more pronounced when attention was directed toward the hemifield contralateral (rather than ipsilateral) to the cluster location (left cluster: $p = .007$; right cluster: $p = .008$; see Figure 3). The two clusters' mean power difference (as an index of posterior alpha power lateralization following spatial attention shifts), however, did not seem to be related to performance in either of the two tasks as suggested by non-significant frequentist correlation tests and Bayesian

statistics ($r_{counting}$ (27) = −.14, $p = .242$, $BF_{01} = 2.40$; $r_{matching}$ (27) = .01, $p = .480$, $BF_{01} = 6.18$). Together, these results suggest that static alpha power modulations, despite representing a prominent feature of the EEG signal, were probably of only minor behavioral relevance in both of our two tasks.

3.3 | Dynamic alpha power

In addition to the static alpha power lateralization following spatial attention shifts, our dynamic alpha power analysis revealed time-dependent modulations of posterior alpha power associated with temporal attention shifts: More specifically and in line with our hypotheses and the anticipated participant strategy to exploit the predictive nature of the stimulus rotation to predict task-relevant points in space and time and to direct attention accordingly, we found a right parieto-occipital electrode cluster that showed a trend toward reduced power in a low alpha frequency range (around 7–10 Hz) shortly before the target orientation was presented on the cued-left side of the screen ($p = .067$, corresponding to a cluster starting around 220 ms before orientation onset; see Figure 4). A similar decline around the target orientation was observed over left parieto-occipital electrodes for stimuli presented on the uncued-right side of the screen but in a lower frequency range around 5–8 Hz ($p = .026$, corresponding to a cluster from −230 to +100 ms around orientation onset). The target orientation of the cued-right and the uncued-left side of the screen, in contrast, was not associated with dynamic power modulations toward task-relevant points in time, nor was the non-target orientation irrespective of the locus of attention and stimuli (all cluster p's ≥ .136).

Whereas, left-hemispheric low-frequent power decreases around onset of the target orientation on the uncued-right side of the screen were not related to accuracy in either of the two tasks as suggested by non-significant frequentist correlation tests and Bayesian estimates ($r_{counting}$ (27) = .15, $p = .224$, $BF_{01} = 9.19$; $r_{matching}$ (27) = .16, $p = .203$, $BF_{01} = 7.53$), right-hemispheric alpha power reductions in preparation of the upcoming target orientation on the cued-left side of the screen appeared to be behaviorally relevant for performance in the following delayed match-to-sample task. Stronger alpha power decreases, however, tended to be associated with impaired rather than improved matching performance thereafter ($r_{matching}$ (27) = .28, $p = .068$, $BF_{10}^+ = 1.14$; $r_{counting}$ (27) = .23, $p = .111$, $BF_{01} = 8.85$). This effect seemed to be mainly driven by a poor matching performance for probes of the non-target orientation ($r_{non-target}$ (27) = .33, $p = .040$, $BF_{10}^+ = 1.92$; r_{target} (27) = .16, $p = .208$, $BF_{01} = 3.17$) and for matches between the probed and the actual
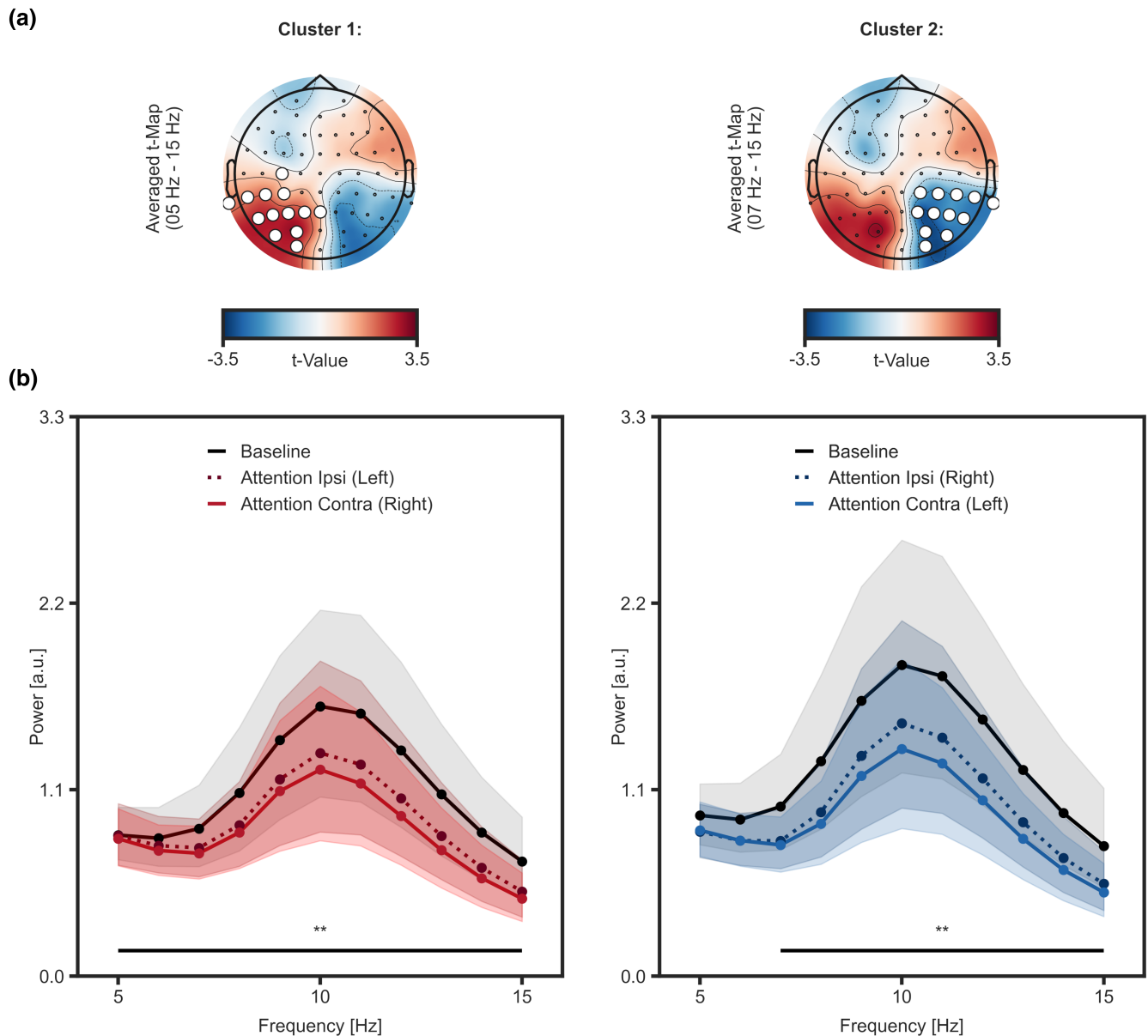
FIGURE 3 Grand-average static power modulation during the dynamic counting task (a) The topographic illustration of *t* values for each of the two identified clusters averaged across the respective frequency bands shows that posterior-parietal electrodes were sensitive to the spatial allocation of attention throughout the rotation of the dynamic counting task; (b) The corresponding spectral plots indicate a decrease of broad-band power (with a peak in the 8–12 Hz alpha frequency range) during the stimulus rotation compared to the inter-trial baseline, which was significantly more pronounced for attention directed at the contralateral hemifield (*Contra*) compared to the ipsilateral hemifield (*Ipsi*). Cluster electrodes are reflected by white circles and 95% confidence intervals by shaded areas in gray. Asterisks indicate statistical significance, where * $\triangleq p < .05$, ** $\triangleq p < .01$ and *** $\triangleq p < .001$.

non-target orientation more specifically as suggested by a highly significant frequentist correlation and Bayesian estimates ($r_{non\text{-}target\text{-}match}$ (27) = .44, $p = .008$, $BF_{10}^{+} = 10.66$; $r_{non\text{-}target\text{-}mismatch}$ (27) = −.09, $p = .319$, $BF_{01} = 3.89$). Together, these results suggest that participants who preferentially allocated attentional resources to locations and time points relevant to the current task at hand (i.e., counting of the target orientation) might have lacked attentional resources for other ongoing and attention-dependent but currently task-irrelevant processes (i.e., maintenance of a

precise non-target memory template), leading to impaired memory fidelity and consequently worse matching performance for the counting-irrelevant non-target orientation thereafter.

3.4 | Event-related potentials

Left–Right difference waves were neither affected by *Orientation* (target vs. non-target; all cluster p's ≥ .184)
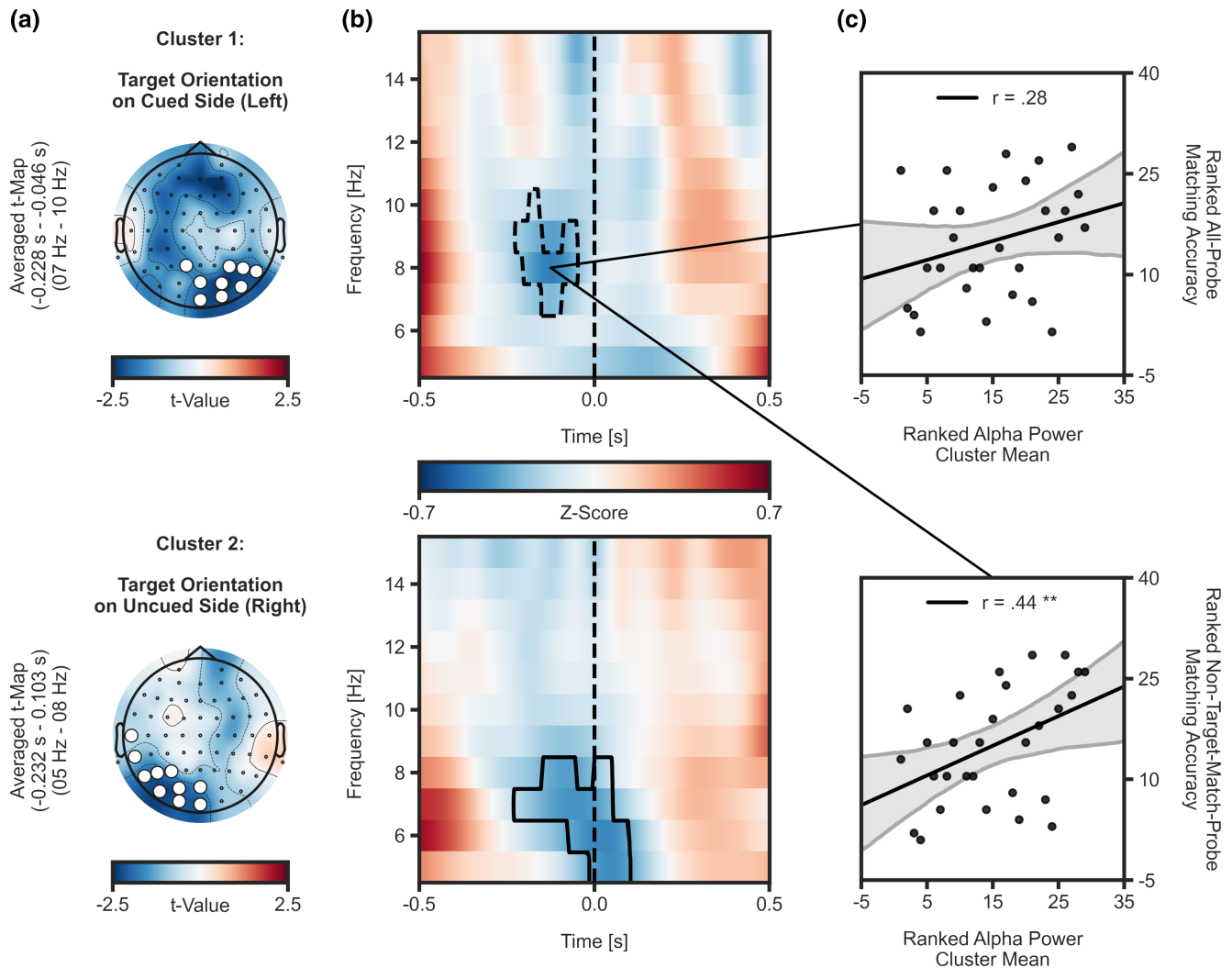
FIGURE 4 Grand-average dynamic power modulation during the dynamic counting task (a) The topographic illustration of *t* values for each of the two identified clusters averaged across the respective time windows and frequency bands shows contralateral, parieto-occipital power decreases for the target orientation on the cued-left and uncued-right side of the screen; (b) The corresponding time-frequency plots show that these power decreases were located in the alpha/theta frequency range and started around 230 ms before onset of the target orientation; (c) The correlation between the ranked strength of right-hemispheric alpha power reductions shortly before onset of the target orientation on the cued-left side of the screen (averaged across electrodes, frequencies and time points) and ranked accuracy in the delayed match-to-sample task (separately for all vs. non-target-match probes) shows a decline in performance (primarily for probes matching the non-target orientation) with increasing alpha power reduction. Cluster electrodes are reflected by white circles, (marginally) significant clusters by solid/dashed black lines and 95% confidence intervals by shaded areas in gray. Asterisks indicate statistical significance, where * ≙ $p < .05$, ** ≙ $p < .01$ and *** ≙ $p < .001$.

nor by *Side* (cued vs. uncued; all cluster *p*'s≥.166). Most importantly, however, we observed three significant *Orientation-by-Side* interaction clusters around centro-parietal electrodes (with a slight right-hemispheric dominance), which showed an increasing negativity toward onset of the target orientation on the cued side of the screen (i.e., toward task-relevant moments in time at task-relevant locations in space calling for attentional prioritization; $p = .034/.007/.052$, corresponding to clusters from approximately −220 to −110 ms, −90 to +190 ms and +210 to +290 ms around onset of the target orientation,

respectively; see Figure 5). No such effect was observed for the target orientation on the uncued side of the screen, nor for the non-target orientation on either side of the screen.

This ERP interaction effect (i.e., an increasing negativity exclusively around onset of the target orientation on the cued side of the screen) was significantly but again positively correlated with performance in the following delayed match-to-sample task: Stronger ERP *Orientation-by-Side* interactions were associated with impaired rather than improved matching performance thereafter as supported by a significant frequentist correlation
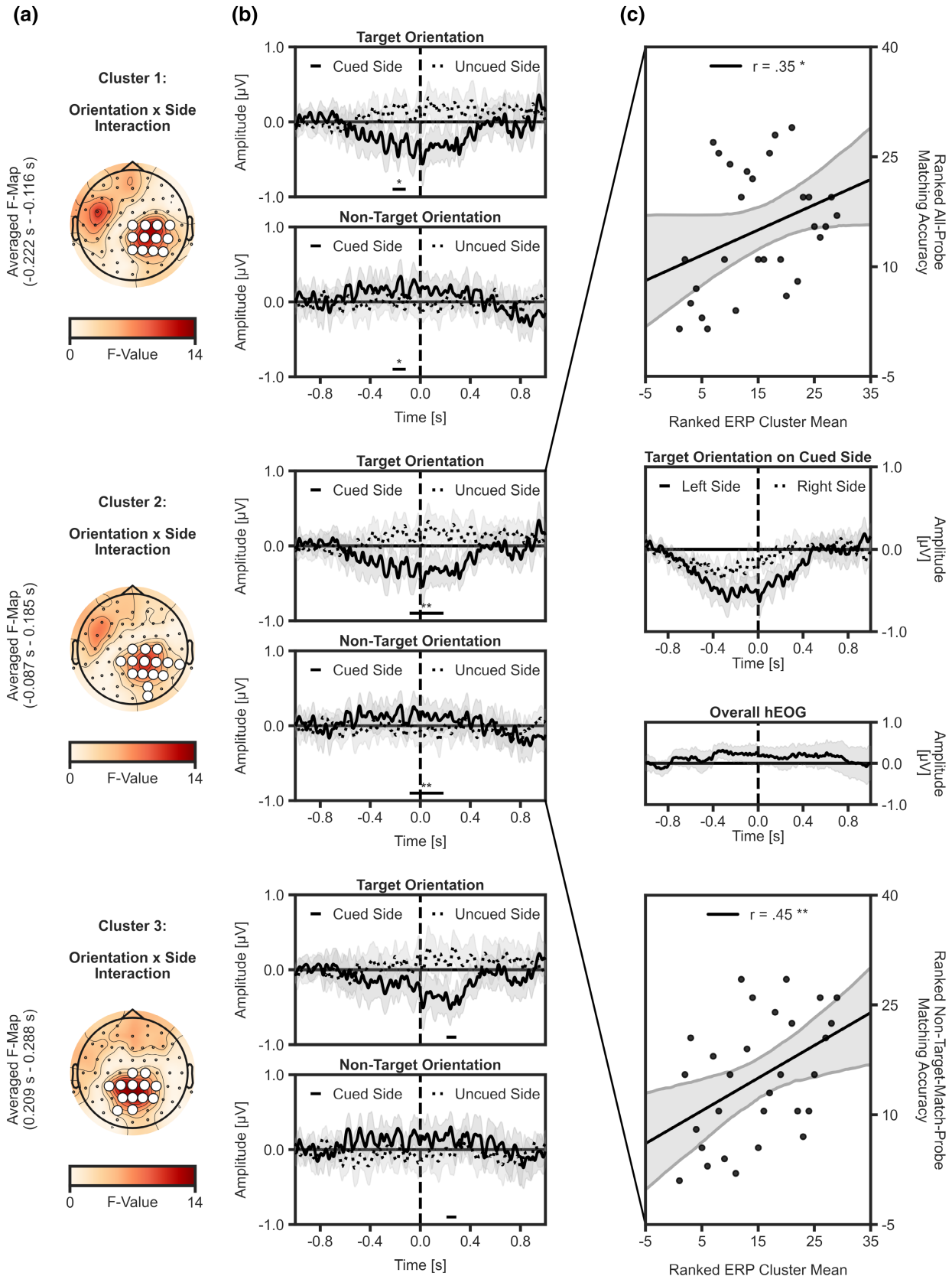
and Bayesian statistics ($r_{matching}$ (27) = .35, p = .033, BF_{10}^{+} = 4.33; $r_{counting}$ (27) = .19, p = .166, BF_{01} = 8.32). As for dynamic alpha power decreases, this effect appeared to be mainly driven by a poor matching performance for

probes of the non-target orientation ($r_{non-target}$ (27) = .29, p = .061, BF_{10}^{+} = 1.34; r_{target}(27) = .21, p = .141, BF_{01} = 2.49) and for matches between the probed and the actual non-target orientation more specifically as supported by a

FIGURE 5 Grand-average event-related potentials (ERPs) during the dynamic counting task (a) The topographic illustration of *F* values for each of the three identified clusters averaged across the respective time windows shows a significant *Orientation-by-Side* interaction of *Left–Right* difference ERPs at centro-parietal electrodes primarily over the right hemisphere; (b) The corresponding ERPs show an increasing negativity toward the target orientation on the cued side of the screen. For the dominant second cluster, this negativity is more pronounced for stimuli presented on the left side of the screen (i.e., contralateral to the cluster location) and independent of eye movements (as indicated by the flat horizontal electrooculogram) (c) The correlation between the ranked strength of the ERP *Orientation-by-Side* interaction around onset of the target orientation on the cued side of the screen (averaged across electrodes and time points of the dominant second cluster) and ranked accuracy in the delayed match-to-sample task (separately for all vs. non-target-match probes) shows a decline in performance (primarily for probes matching the non-target orientation) with increasing ERP negativity. Cluster electrodes are reflected by white circles, cluster time points by horizontal black bars and 95% confidence intervals by shaded areas in gray. Asterisks indicate statistical significance, where * $\triangleq$ *p* < .05, ** $\triangleq$ *p* < .01 and *** $\triangleq$ *p* < .001.

highly significant frequentist correlation and Bayesian estimates ($r_{non\text{-}target\text{-}match}$ (27) = .45, *p* = .007, BF_{10}^+ = 11.54; $r_{non\text{-}target\text{-}mismatch}$ (27) = −.24, *p* = .105, BF_{01} = 2.05). In line with the observed alpha-behavior correlations, this finding seems to suggest that participants who accurately anticipated and attentionally prioritized the location and onset of a task-relevant event (i.e., onset of the target orientation in the cued hemifield) might have experienced a shortage of attentional capacities that were left for currently task-irrelevant but subsequently eventually important processes (i.e., maintenance of a precise non-target memory template throughout the rotation to successfully solve the following delayed match-to-sample task), leading to impaired memorization and thus worse matching performance for probes of the non-target orientation thereafter.

3.5 | Alpha-ERP correlation

In line with the topographical differences between the observed clusters of dynamic alpha power modulations and slow negative potentials (i.e., alpha effects being most pronounced over strongly right-lateralized parieto-occipital electrodes vs. slow wave effects being most pronounced over slightly less right-lateralized centro-parietal electrodes), we found no evidence for a substantial correlation between the observed effects of dynamic alpha power and slow wave negativity (r(27) = .24, *p* = .208, BF_{01} = 2.04). This finding suggests that dynamic alpha power modulations and slow negative potentials presumably do not just reflect different aspects of the same underlying mechanism but instead seem to constitute two individual signatures of spatio-temporal attention.

4 | DISCUSSION

Alpha power modulations and slow negative potentials have previously been associated with anticipatory processes in spatial and temporal top-down attention (Di

Russo et al., 2021; Hanslmayr et al., 2007; Praamstra et al., 2006; Rohenkohl & Nobre, 2011; Sauseng et al., 2005; Zanto et al., 2011). In traditional experimental paradigms, however, externally triggered neural activity in response to attention-directing cues or response-demanding targets and the associated decision- and motor-related processes constitute potential confounds for the detection and interpretation of subtle neural changes following spatio-temporal attention shifts. In the present study, we investigated alpha power changes and slow negative waves during simultaneous shifts of attention in space and time while participants performed a dynamic target detection task, which was not only free from potentially confounding stimulus-driven alpha power fluctuations and evoked neural responses but also designed to minimize decision- and motor-related processing enabling a confined analysis of preparatory processes on the perceptual level. We hypothesized that participants would naturally and dynamically guide attention to task-relevant moments in time (i.e., onset of the target orientation) at task-relevant locations in space (i.e., in the cued hemifield); and that such spatio-temporal attention shifts would be reflected by dynamic alpha power decreases and slow negative potentials over posterior electrodes contralateral to the locus of attention.

In line with this hypothesis and previous reports of alpha power decreases following spatial and temporal attention shifts (Heideman et al., 2018; Popov et al., 2019; Rohenkohl & Nobre, 2011; Sauseng et al., 2005; van Ede et al., 2020; Zanto et al., 2011), we observed a reduction in alpha power over right, parieto-occipital electrodes shortly before onset of the target orientation on the attended, cued-left side of the screen. Importantly, in contrast to the static alpha power lateralization that was observed throughout the stimulus rotation but that was not related to performance in either of the two tasks, this dynamic alpha power decrease (despite being a statistical trend and of much less significance than the static alpha effect) appeared to be relevant for performance in the subsequent delayed match-to-sample task (which required high visual acuity and was thus presumably more

sensitive to individual differences in spatio-temporal attention tuning than the comparatively easy, uncorrelated dynamic counting task). Our observation that strong alpha power decreases around task-relevant points in space and time (indicative of an attentional prioritization of currently task-relevant information) were detrimental rather than beneficial to matching accuracy may seem contradictory at first. The finding that this adverse relationship was primarily driven by (matching) probes of the non-target orientation (whose successful recognition required the maintenance of a precise non-target memory template throughout the stimulus rotation, creating strong competition for limited attentional resources with the counting-relevant target orientation), however, is well in line with the existing evidence for a close interaction between attention and working memory processes (Awh et al., 2006; Feng et al., 2012; Vogel et al., 2005). The reported correlation might thus be best explained in terms of a detriment for memories of previously task-irrelevant and thus unattended information (Griffin & Nobre, 2003; Schmidt et al., 2002). Our alpha power findings suggest that participants can naturally and dynamically allocate attentional resources to task-relevant points in space and time, which might, however, come at the expense of reduced attentional resources and impaired behavioral performance for information outside the current focus of attention. Such spatio-temporal attention tuning appears to be reflected by dynamic alpha power decreases around prioritized moments in time over visual cortices contralateral to prioritized locations in space.

Interestingly, it has recently been suggested that, due to their link to intrinsic fluctuations in perception and attention (Helfrich et al., 2018; Landau & Fries, 2012; Plöchl et al., 2022), theta oscillations might be particularly sensitive to temporal shifts of top-down attention, whereas alpha oscillations were found to be dominated by spatial attention effects instead (Meehan et al., 2021). Although we, too, observed a significant power modulation in the theta frequency range over left, parieto-occipital electrodes when the stimulus rotation on the right side of the screen reached the target orientation, this effect (in our case a power decrease in contrast to the increase that was reported by Meehan et al., 2021) was found for the unattended screen half and, in contrast to the observed alpha cluster, was apparently not related to performance in either of the two tasks. If and to what degree these inconsistencies can be attributed to the specific task designs or the advantages and potential disadvantages associated with such can only be speculated on. Based on the notion that there might not be *the* way in which temporal attention operates (Nobre & van Ede, 2018; van Ede et al., 2020), it is well possible that although theta oscillations might be particularly susceptible to externally driven temporal

attention shifts in the absence of spatial expectations (such as in the study by Meehan et al., 2021), during internally driven shifts of combined spatio-temporal attention (such as in the present experiment) they could take over a subordinary role (e.g., dynamically suppressing sampling mechanisms for currently irrelevant information to protect task-relevant processing from potential interference) and might be replaced by dynamic alpha power modulations as dominant signature instead.

In previous studies, short-term fluctuations of perception have mainly been associated with the phase rather than with the amplitude of alpha and other low-frequent oscillations (Busch et al., 2009; Busch & VanRullen, 2010; Hanslmayr et al., 2011; Landau & Fries, 2012; Zauner et al., 2012), which reflects intrinsic fluctuations between states of high versus low excitability thereby affecting subsequent information processing (Buzsáki & Draguhn, 2004; Haegens et al., 2011; van Diepen et al., 2015; Zoefel & VanRullen, 2017). Alpha power suppression, however, has been proposed to shorten the inhibitory phase associated with impaired signal processing (Jensen & Mazaheri, 2010; Mazaheri & Jensen, 2010; Peylo et al., 2021) and the effect of oscillatory phase has been reported to be diminished under low alpha power accordingly (Fakche et al., 2022; Mathewson et al., 2009). A dynamic and transient reduction of alpha power shortly before the onset of a task-relevant stimulus might therefore help reduce effects of alpha phase, thereby stabilizing perception at relevant moments in time (just as it has recently been proposed for saccadic eye movements and similar to previous suggestions of oscillatory desynchronization as active mechanism that supports sharp and information-rich long-term memories; Denison et al., 2019; Hanslmayr et al., 2012; Hanslmayr et al., 2016). A direct test of this interpretation, however, was beyond the scope of the present paper and remains a matter for future research.

In addition to dynamic alpha power modulations, we observed a slow and negative *Left–Right* difference potential over right-lateralized, centro-parietal electrodes, which increased toward and then peaked around onset of the target orientation on the cued side of the screen (with a maximum negativity for stimuli presented in the contralateral, left hemifield). The observation of an anticipatory negative wave in a paradigm that was designed to minimize decision- and motor-related processes, which was further correlated with subsequent memory performance, argues against the traditional view that slow negative potentials in anticipation of an upcoming, task-relevant event primarily reflect preparatory processes on the level of response decision and execution (Griffin et al., 2001, 2002; Miniussi et al., 1999; Nobre, 2001). Instead, our finding seems to support the notion of a temporal attention-driven sensory

preparation reflected by slow negative waves (Bianco et al., 2020; Correa et al., 2006; Di Russo et al., 2019, 2021; Rohenkohl et al., 2012). Although we cannot entirely exclude the possibility that participants, even though not instructed to, made subtle movements or intermediate response decisions while mentally counting task-relevant events (i.e., onset of the target orientation on the cued side of the screen) leading to the observed negative potential, this alternative explanation seems unlikely for the following reasons: Since potential auxiliary movements would have probably been executed either with the dominant or the task-related hand (both of which correspond to the right hand for the large majority of our sample and the present target detection task), effects of response preparation and/or execution should have been elicited primarily over central electrodes of the left hemisphere. Moreover, perception-unrelated preparatory processes on the level of response decision and execution should have occurred independently of the stimulus location (i.e., they should have been equally strong for the target orientation on the cued-left and the cued-right side of the screen) and they should have been unable to affect subsequent memory performance. Instead we observed stronger contralateral negativity over right-hemispheric, centro-parietal electrodes, which was significantly correlated with accuracy in the following delayed match-to-sample task (although again with an adverse effect on performance, especially for matching probes of the counting-irrelevant non-target orientation). We interpret this finding in line with alpha power reduction as an attention-driven preparation of task-relevant cortices including the visual hierarchy for relevant points in space and time at the cost of reduced attentional resources and impaired behavioral performance for information outside the current focus of attention.

Our findings of dynamic alpha power decreases and slow negative potentials toward task-relevant moments in time at task-relevant locations in space over electrodes contralateral to the locus of attention (which also appeared to be relatively uncorrelated with one another) provide electrophysiological evidence for a close interaction between spatial and temporal top-down attention with posterior alpha power and slow negative waves as two largely independent signatures of spatio-temporal attention shifts. This interaction between spatial and temporal top-down attention seems to be of particular relevance for the visual system, which has previously been proposed to be less sensitive to temporal information than other sensory systems due to its retinotopic organization and consequent preference for spatial information and which has thus been suggested to be indirectly impacted by temporal attention through the modulation of retinotopically

specific spatial attention effects (Correa et al., 2006; Doherty et al., 2005; Nobre, 2001; Nobre & van Ede, 2018; Rohenkohl et al., 2014). Using a paradigm free from potentially confounding stimulus-driven alpha power fluctuations and evoked neural responses, we revealed subtle attention-driven alpha power dynamics, which seemed to be more informative of behavior than the much stronger and more commonly investigated static alpha power lateralization effects. Such dynamic alpha power modulations might constitute a universal mechanism for the flexible prioritization of information at its most relevant moments in time, independent of the sensory modality (van Ede et al., 2011; Wöstmann et al., 2021) and whether the attentional spotlight shines at information in the external or internal space (de Vries et al., 2017; van Ede et al., 2017). Since our paradigm was also designed to minimize decision- and motor-related processing, our finding of slow negative potentials and their non-trivial correlation with subsequent memory performance further adds to the growing evidence that temporal attention can affect cognitive processes beyond the level of response preparation and execution and suggests that such processes might be reflected by slow negative waves. Although it should be noted that some of our findings represent statistical trends and partially provide only weak evidence for the alternative hypothesis and should thus be interpreted with caution until further replication, we would like to point out that small effects are well in line with the proposed preference of the visual system for spatial over temporal information and are to be expected given the complexity of our paradigm with multiple events taking place in close spatial and temporal proximity during a continuous visual stimulation that might have reduced alpha power to a minimal level already, thereby reducing the possibility to observe strong attention-related alpha power desynchronization beyond this point (Kelly et al., 2006). We would also like to emphasize that our results are not meant to imply that temporal attention exclusively acts on the perceptual level, nor that attention-driven decision- and motor-related processes or static alpha power lateralization effects are in any way less meaningful or important. We do, however, believe that it is important to investigate the same phenomena from different perspectives using different paradigms to reveal all of the components potentially contributing to complex real-life behavior and therefore hope that our study inspires other researchers to move beyond classical experimental paradigms to broaden our understanding of spatio-temporal shifts of visual top-down attention.

AUTHOR CONTRIBUTIONS

Charline Peylo: Conceptualization; data curation; formal analysis; investigation; methodology; project

CONFLICT OF INTEREST STATEMENT
The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT
The data that support the findings of this experimental study are available from the corresponding author upon reasonable request.

ETHICS STATEMENT
The study was approved by the Ethics Commission of the Faculty of Psychology and Education of the Ludwig-Maximilians-Universität München and was conducted in accordance with the Declaration of Helsinki. Informed consent was obtained from all individual participants included in the study.

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