

## Neurophysiological processes reflecting the effects of the immediate past during the dynamic management of actions

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### ABSTRACT

In recent years, there has been many efforts to establish a comprehensive theoretical framework explaining the working mechanisms involved in perception-action integration. This framework stresses the importance of the immediate past on mechanisms supporting perception-action integration. The present study investigates the neurophysiological principles of dynamic perception-action bindings, particularly considering the influence of the immediate history on action control mechanisms. For this purpose, we conducted an established stimulus-response binding paradigm during EEG recording. The SR-task measures stimulus-response binding in terms of accuracy and reaction time differences depending on the degree of feature overlap between conditions. Alpha, beta and theta band activity in distinct time domains as well as associated brain regions were investigated applying time-frequency analyses, a beamforming approach as well as correlation analyses. We demonstrate, for the first time, interdependencies of neuronal processes relying on the immediate past. The reconfiguration of an action seems to overwrite immediately preceding processes. The analyses revealed modulations of theta (TBA), alpha (ABA) and beta band activity (BBA) in connection with fronto-temporal structures supporting the theoretical assumptions of the considered conceptual framework. The close interplay of attentional modulation by gating irrelevant information (ABA) and binding and retrieval processes (TBA) is reflected by the correlation of ABA in all pre-probe-intervals with post-probe TBA. Likewise, the role of BBA in maintaining the event file until retrieval is corroborated by BBA preceding the TBA-associated retrieval of perception-action codes. Following action execution, TBA shifted towards visual association cortices probably reflecting preparation for upcoming information, while ABA and BBA continue to reflect processes of attentional control and information selection for goal-directed behavior. The present work provides the first empirical support for concepts about the neurophysiological mechanisms of dynamic management of perception and action.

### 1. Introduction

Imagine you are always buying a coffee from a specific café every morning. Every time you see the café sign, you walk in and order coffee. One evening, you decide to not buy coffee anymore and opt for tea instead. The next day, you come across the familiar café sign. Your first impulse then is to go in and order coffee. However, in the café, and remembering your decision, you actively choose to order tea instead.

This example describes how we have to overcome established stimulus-response associations in everyday life in order to behave differently in otherwise identical situations. This requires a flexible management of stimulus-response associations and the top-down control.

A recent conceptual framework detailing the management of established stimulus-response associations is the Binding and Retrieval in Action Control (BRAC) framework (Frings et al., 2020) reflecting a modern version of ideomotor theory and the Theory of Event Coding

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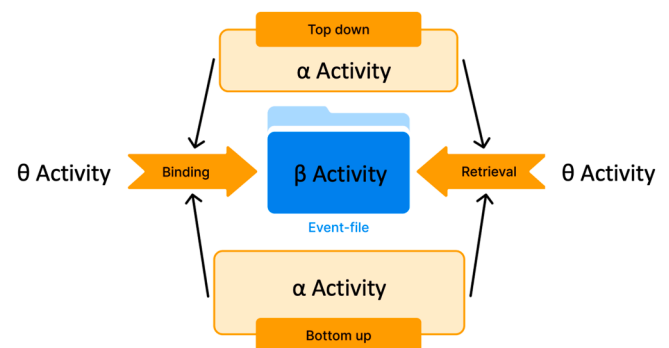
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(TEC) (Frings et al., 2020; Hommel et al., 2001). Similar to TEC, BRAC considers that stimulus-response associations are stored in so-called event files (Frings et al., 2020). More specifically, features of a stimulus (e.g., color, orientation, shape) are combined in an “object file”, whereas action features (e.g. direction of a movement and which limb to use etc.) are stored in an “action file”. Object and action files are combined and stored in a common “event file” if they occur in close temporal proximity (Frings et al., 2020). According to BRAC and TEC, the formation of the event file is further influenced by other (top down and bottom up) factors, such as attention or memory effects, the salience of the stimulus or task instruction. Once formed, event files can be reactivated due to their network structure, when stimuli, actions or their associated effects are re-encountered. As soon as a single element contained in the event file reappears, the entire event file is retrieved. The retrieval of a previously created event file can facilitate or hamper subsequent actions, depending on the fit with the currently required response and the need to reconfigure the event file. Reconfiguration refers to discarding existing bindings within an event file and the creation of new links. Experimentally, this is usually investigated by prime-probe structured experiments (Frings et al., 2020), where an event file is bound at the prime and retrieved at the time of the probe stimulus. Importantly, as an extension of TEC, BRAC allows the explicit distinction between binding (i.e., integration of stimulus and action features occurring in temporal proximity into an event file) and retrieval of event files (when an event file is reactivated through re-encountering at least one of the elements included in the event file). Several studies have already validated the distinction between binding and retrieval on the basis of behavioral data (Foerster et al., 2021; Frings et al., 2022; Laub et al., 2018; Mocke et al., 2022; Qiu et al., 2022; Schmalbrock and Frings, 2022). Schmalbrock and Frings (2022), for example, distinguished between the effects of experimental figure-ground manipulations in a distractor-response-binding task on binding and retrieval. They found that retrieval processes in particular were affected, which supports the differentiation between the two processes (Schmalbrock and Frings, 2022). However, it is unknown how these binding and retrieval processes are implemented on a neurophysiological level, i.e. which neurophysiological subprocesses and functional neuroanatomical structures underlie binding and retrieval processes. For this purpose, focusing solely on post-probe processes is insufficient. Recent research has highlighted the impact of pre-stimulus activity on post-stimulus processes using various methodological approaches (Wainio-Theberge et al., 2021; Wolff et al., 2019, 2021). Wolff et al. conducted a study on patients with drug-resistant epilepsy using stereotactic electroencephalography. The results showed that poststimulus effects, such as trial-to-trial variability reduction, are not exclusively driven by the stimulus itself, but are also significantly influenced by prestimulus dynamics. They found that earlier poststimulus processes are more strongly influenced by prestimulus dynamics (0–300 ms) than later ones (Wolff et al., 2021), demonstrating the significance of the immediate past for post-probe processes (Wainio-Theberge et al., 2021; Wolff et al., 2019). He et al. (2013) also highlighted the significance of prestimulus activity for poststimulus activity, illustrated by reduced evoked post-stimulus activity following higher prestimulus activity as measured by functional magnetic resonance imaging, (He, 2013). Taking into account the procedural nature of action planning and execution which is reflected in paradigms used for studying motor control (Beste et al., 2023), it becomes apparent that it is insufficient to consider only post-probe (action execution) processes when examining processes involved in binding and retrieval or action control in general. In order to achieve a comprehensive understanding and distinction of the processing stages and neurophysiological mechanisms involved in binding and retrieval of integrated perception-action representations (i.e. event files), it is crucial to also incorporate processes occurring in the immediate past before a trial and during inter-trial intervals. Event file binding is often measured by the stimulus-response (SR) task (Colzato et al., 2006), which manipulates the extent to which stimulus and response features

overlap to measure binding effects. The procedural nature of the SR task (cue - prime - probe- structure) takes account of the importance to include the immediate past before the probe, rather than exclusively considering processes after the probe. Recent studies have provided evidence regarding the significance of the interplay between theta and alpha activity in the phase preceding action selection and even during idling periods between trials (Prochnow et al., 2022; Wendigens and Beste, 2023).

A very recent account (Beste et al., 2023) has linked distinct patterns of neural oscillatory activity to the cognitive processes specified in the BRAC framework. Fig. 1 specifies the assumptions of how alpha, beta and theta oscillations might interact during action control processes as claimed by BRAC.

In particular, it has been suggested that binding and retrieval processes very much depend on theta band activity (TBA) and that alpha band activity (ABA) modulates these TBA dependent binding and retrieval processes (Beste et al., 2023). This BRAC-interpretation can readily be reconciled with biophysical principles of TBA facilitating the integration of information between distant functional neuroanatomical regions (Buzsáki and Draguhn, 2004) and currently assumed computational principles of TBA likely reflecting a signal that initiates adaptive processes (Cavanagh and Frank, 2014). ABA in turn reflects effects of top-down and bottom-up attentional control processes known to modulate event file dynamics (Frings et al., 2020). This assumed role of ABA is in line with the influential “inhibition timing hypothesis” (Klimesch, 2012; Klimesch et al., 2007). Several lines of evidence have already shown TBA and ABA to be involved in event file dynamics (Dilcher et al., 2021; Opitz et al., 2020; Prochnow et al., 2022, 2022; Takacs et al., 2020a). These data showed that TBA and ABA are relevant for the formation and retrieval of event files, but not their maintenance/stability (i.e., the preservation of the characteristics of an event file from formation until retrieval), which are likely a function of beta band activity (BBA) (Beste et al., 2023; Pastötter and Frings, 2018). Once an event file has been created (bound) BBA ensures its stability /maintainance until it is retrieved. This conception is in keeping with the notion that BBA reflects changes from active to latent to re-activated states (Spitzer and Haegens, 2017). Transferred to dynamic event file management according to BRAC, this means that high BBA might represent the transition of a latently existing into an active event file, for example, in case features of the event file re-occur and thus have to be reactivated (Beste et al., 2023). Crucially, the relative contribution of TBA, ABA und BBA during event file binding and retrieval processes is elusive and hence the neural basis of central mechanistic elements of BRAC. This notwithstanding, Beste et al. (2023) provide clear and



**Fig. 1.** Overview on oscillatory activity and interrelations based on Beste et al. (2023). It is suggested that TBA is primarily involved in binding and retrieval processes, while ABA is involved in the modulation of these processes. BBA is likely associated with the maintenance/stability of an event file in terms of latent memory traces. Therefore, it can be assumed that ABA and TBA should correlate during binding and retrieval. According to the model, however, there should be no association between ABA and BBA. However, a correlation between TBA and ABA can be assumed.

testable hypotheses regarding the relevance and relative contribution of TBA, ABA and BBA for event file binding and retrieval processes.

With regard to the level of activity in the frequency bands under consideration, the following hypotheses are proposed: Based on the results of Prochnow et al. (2022), who observed an opposing relationship between TBA and ABA depending on the need to reconfigure an event file, we assume that a modulation of TBA / ABA can particularly be observed whenever a reconfiguration of an event file is required. In this case, we expect ABA to be weaker. Furthermore, if no reconfiguration is required, high ABA and low TBA is to be expected (Prochnow et al., 2022). BBA should be high when features of the event file re-occur (i.e., have to be re-activated). Prior research suggests that frontoparietal networks as well as parieto-occipital interactions, play a pivotal role in the retrieval phase of event file coding (Chmielewski and Beste, 2019; Dilcher et al., 2021; Friedrich et al., 2020; Kleimaker et al., 2020; Opitz et al., 2020; Prochnow et al., 2022; Wendiggensen et al., 2023).

Regarding the interrelations between frequency bands and over different time periods, the following is expected: According to the postulated interrelations, TBA at the time of binding and during retrieval should correlate. Furthermore, it can be assumed that ABA modulating binding and retrieval processes (Beste et al., 2023), should be correlated with TBA during binding and retrieval. In contrast, given that BBA is associated with the maintenance rather than modulation of event files it should not correlate with ABA but might correlate with TBA at the time of retrieval.

In order to investigate the specific function of the mentioned frequency bands in action control according to BRAC, this study considered different time windows in a sequential event file coding paradigm. First, the strength of the TBA, ABA and BBA in the different task sections was examined using time-frequency analyses. Next, the sources of activity were localized using a beamforming approach. Finally, correlation analyses were carried out using the different time ranges and frequency bands. The correlation analyses are run on the level of reconstructed sources. Through this, the functional relevance of neuroanatomical regions becomes further elucidated and closely connected to neurophysiological principles supporting goal-directed actions as specified by a recent and behaviorally well-validated cognitive science concept of action control (Beste et al., 2023).

## 2. Methods

### 2.1. Participants

The current analysis comprises datasets of  $N = 55$  healthy individuals who carried out a stimulus (S)-response (R) binding task (Beste et al., 2021; Dilcher et al., 2021; Kleimaker et al., 2020) as part of different studies. The data collection for the different studies was conducted at various locations using the same recording and experimental equipment. Four participants were excluded from further analysis due to significantly lower accuracy rates in the behavioral data (achieving less than 50 % accuracy in at least one of the conditions). The remaining sample of  $N = 51$  individuals included 19 men and 32 women, with an average age of 24 years ( $SD = 3.2$  years), spanning an age range of 18 to 33 years. Comparable investigations employing the methodological approach in the past have employed similar or smaller sample sizes (Wendiggensen et al., 2022; Wendiggensen and Beste, 2023). Thus, this study aligns with prior published research and is presumed to possess sufficient statistical power. All participants were right-handed and had normal or corrected-to-normal vision. They were also not taking any medication that could affect the neurophysiological processes under investigation and stated that they had no history of psychiatric or neurological conditions.

Prior to the experiment, all participants provided written informed consent. The study received ethical approval from the local ethics committee of the Medical Faculty of TU Dresden and the University of Lübeck and was carried out in accordance with the Declaration of

Helsinki.

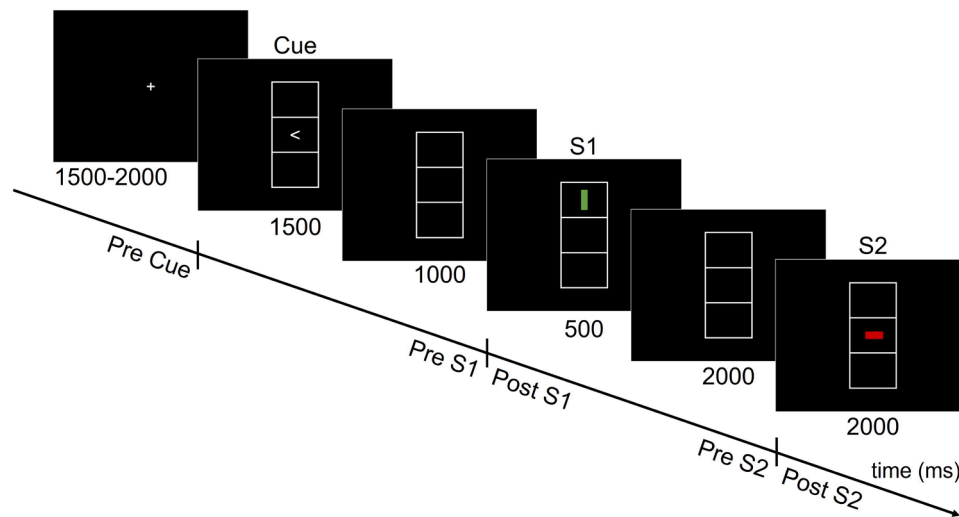
### 2.2. Task

We used an established paradigm (Colzato et al., 2006) to measure event-file coding. The paradigm is illustrated in Fig. 2.

Participants were positioned in front of a 25-inch screen, maintaining a viewing distance of 60 cm. They were presented with a rectangle, measuring 6.7 cm x 2.8 cm. This rectangle consisted of three vertically arranged boxes of equal height. At the onset of each trial, an arrowhead pointing to the left or to the right was exhibited within the central box for a duration of 1500 milliseconds, serving as the cue stimulus. Following this, a blank screen was displayed for 1000 milliseconds, superseded by the appearance of the rectangle, in which then stimulus S1 (= prime) appeared in the upper or lower box. S1 could either be a horizontal or vertical bar colored red or green. The orientation, color, and location of S1 was randomized, and its display persisted for 500 milliseconds. Subsequently, the screen remained blank for 2000 milliseconds before the appearance of S2 (= probe), exhibiting the same randomly varied attributes as S1. Two conditions of feature overlap between S1 and S2 are possible: complete feature overlap (S1 and S2 were identical in terms of position, color and orientation) or no feature overlap. Within each trial, participants were required to perform two responses (R1, R2). Using their corresponding index fingers, they had to press the left or right control key on a computer keyboard. For R1 participants had to memorize the direction of the cue (arrowhead pointing left or right). It is important to stress out that participants were instructed to only indicate the direction of the cue stimulus at the time S1 appeared. In terms of BRAC, an event file is created at this point by linking the stimulus features of S1 to the required action indicated by the direction of the arrowhead (press right or left). Following this, participants were required to promptly respond to S2 indicating the orientation of the presented bar. In case of a horizontal alignment, participants had to press the left key and vertical line required to press the right key. At this point, the previously created event file is retrieved if an element of the event file (consisting of S1 and R1) is repeated, either by a matching stimulus feature or a matching response. The entire task consisted of 192 trials, distributed across six blocks of 32 trials, respectively. In the time interval between trials, a fixation cross was displayed at the center of the screen and its duration varied between 1500 and 2000 milliseconds. Throughout the task, reaction times and response accuracy were recorded.

The task sequence allows the distinction of four conditions. Responses to S2 and S1 ( $R1 = R2$ ) can either be the same (response repetition) or different (response alternation). Correspondingly, the stimulus properties of S1 and S2 can match (full feature overlap) or not (no feature overlap). The combination of these factors results in four conditions (stimulus feature overlap x response repetition, stimulus feature overlap x response alternation, no stimulus feature overlap x response repetition, no stimulus feature overlap x response alternation). The condition can thus only be determined after S2 has appeared.

The event file is not reactivated (= not retrieved) in the condition in which there is no overlap of stimulus features and the requirement of an alternating response. In all other conditions, the event file is reactivated by repeating some or all of its features. If there are only partially overlapping characteristics (stimulus feature overlap x response alternation and no stimulus feature overlap x response repetition), the event file must be reconfigured. The event file can only remain unchanged if the characteristics match completely, which is only the case for the stimulus feature overlap x response repetition condition. The experimental design thus allows measuring event file binding in terms of costs or benefits depending on the combination of stimulus and response features. In case of full feature overlap and response alternation, the event file has to be reconfigured resulting in higher reaction times and higher error rates/lower accuracy (repetition costs), while in case of full feature overlap and response repetition, the pre-existing link between stimulus features



**Fig. 2.** Schematic illustration of a trial in the stimulus (S) – response (R) – paradigm introduced by Colzato et al. (2006). The investigated time intervals are depicted along the timeline. Each interval is 1000 ms in length. The pre-cue interval comprises the period before the appearance of the cue stimulus (–6000 to –5000 ms prior to the appearance of S2). The pre-S1 interval encompasses the period from 3500 - 2500 ms and the post-S1 interval the segment from 2500 - 1500 ms before the onset of the S2. The investigated pre-S2 interval includes the time span of 1000 ms prior to S2 (= probe) and the post-S2 interval (= within trial) consists of 1000 ms following probe onset. The participants were required to recollect the direction of the cue. Upon the appearance of S1, the participants were to indicate the direction of the cue by pressing either the right or left control button. Upon the appearance of S2, they were to indicate whether the bar was oriented horizontally (left control button) or vertically (right control button).

and response promotes a faster response and lower error rate/ higher accuracy since no reconfiguration is necessary (repetition benefit). Furthermore, no feature overlap and response alternation results in faster responses and fewer errors/ higher accuracy than no feature overlap and response repetition since in the latter case, the pre-existing event file has to be reconfigured again (Beste et al., 2021; Dilcher et al., 2021; Kleimaker et al., 2020).

### 2.3. EEG recording and processing

A high-density electroencephalogram (EEG) was recorded using 60 Ag/AgCl electrodes (EasyCap, Wörthsee, Germany) in equidistant positions employing a BrainAmp DC amplifier (Brain Products, Gilching, Germany). The reference and ground electrodes were situated at coordinates  $\theta = 58$ ,  $\varphi = 78$ , and  $\theta = 90$ ,  $\varphi = 90$ , respectively. A sampling rate of 500 Hz was utilized and all electrode impedances were maintained below 5 k $\Omega$ . Brain Vision Analyzer II (Brain Products, Gilching, Germany) was used to conduct initial data preprocessing. Data was downsampled to 256 Hz, followed by band-pass filtering (IIR filter: 0.5 Hz to 40 Hz, order of 8). The EEG data were screened for channels that did not provide any signal or interfering very distorted signal. Channels that met these criteria were removed, which applied to one electrode on average ( $M = 1.23$ ,  $SD = 1.33$ ). The data were then re-referenced to an average reference to minimize the impact of noise sources (artifacts) and improve the signal-to-noise ratio. Subsequent to this, a manual inspection of the data was performed in order to eliminate technical artifacts (for example infrequent, large artifacts like muscle activity). An independent component analysis (Infomax algorithm) was applied to remove residual frequent artifacts, including eye movements, and pulse-related artifacts. Another manual data inspection was performed to exclude remaining artifacts. Finally, removed channels were interpolated by a spherical technique. Upon completing the preprocessing, the subsequent analysis of the EEG data was done using the FieldTrip toolbox (Oostenveld et al., 2010). The data were segmented into epochs centered around the onset of S2. Only correct trials were included in the analysis (both R1 and R2 correct). The epochs were 9000 ms in length, spanning from 7000 ms before S2 onset to 2000 ms after. This length ensured that all stimuli contained in a trial (i.e. cue, S1 and S2), as well as the associated motor responses, were included in one segment. Segments with

persistent distortions were automatically discarded based on these criteria: amplitude variations surpassing 150  $\mu\text{V}$  within a 200 msec window, amplitudes that go beyond 150  $\mu\text{V}$ , and signals beneath 0.5  $\mu\text{V}$  for a duration of 100 ms. After all pre-processing steps, an average of 139.43 trials ( $SD = 19.37$ ) remained for each participant.

The time-frequency analysis was performed utilizing Morlet wavelets with a width of 5 Gaussians and a Hanning taper. The segmented epochs were categorized into five time intervals of interest, each lasting 1000 ms, all referenced to the onset of S2: a pre-cue (–6000 to –5000 ms), pre-S1 (–3500 to –2500 ms), post-S1 (–2500 to –1500 ms), pre-S2 (–1000 to 0 ms), and within-trial interval (0 to 1000 msec). Equal time intervals of 1000 ms each facilitated valid comparisons between different intervals in subsequent analyses. Average power within the beta (12 – 30 Hz), theta (4 – 7 Hz), and alpha (8–12 Hz) frequency band was computed for each electrode and time point. Comparisons were performed between two levels of feature overlap (zero vs. full) for both the response repetition and response alternation conditions. To achieve this,  $t$ -tests were calculated for each time point within the 0 to 1000 ms window relative to S2 onset. P-values were adjusted for multiple comparisons using false discovery rate (FDR) correction (Benjamini and Hochberg, 1995).

### 2.4. EEG beamforming analysis

Using a multistep beamforming strategy that has previously been established in other investigations, source activity time courses were reconstructed from the sensor-level EEG data (Adelhöfer and Beste, 2020; Wendiggensen and Beste, 2023). This approach involved a sequence of two distinct beamformers. First, Dynamic Imaging of Coherent Sources (DICS) beamforming (Gross et al., 2001) was used to identify areas with significant activity differences across task conditions within the frequency domain. Following this, a Linear Constraint Minimum Variance beamformer (LCMV; Van Veen et al., 1997) was utilized to derive the temporal patterns in the alpha (8–12 Hz), beta (13–30 Hz), and theta (4–7 Hz) frequency bands. The extraction took place within the Regions of Interest (ROIs) pinpointed during the primary DICS beamforming phase. The application of the DICS beamformer entailed utilizing a shared spatial filter across the pre-probe period (from pre-cue to pre-S2 interval) and the within-trial interval. For the within-trial

period, the common spatial filter was employed for the two levels of feature overlap in conjunction with both response alternation and repetition conditions. For the pre-probe interval, the distinction between different conditions (full/no feature overlap and response repetition/alternation) could not be made, as the condition of the current trial could not be determined at this point. This distinction becomes only possible with the appearance of the S2. The creation of the common filter was based on the cross-frequency spectrum of averaged power within the relevant frequency band (alpha, beta, or theta). This power was obtained through a fast Fourier transform of the combined overlap levels paired with response alternation and repetition. The data were subsequently projected onto an evenly spaced 0.5 cm grid, derived from the forward-model template offered by the FieldTrip toolbox. Theta, beta, and alpha power values were extracted for all conditions (no/full feature overlap and response repetition/alternation) across all time intervals of interest. To allow for comparison, the source power differences among the four conditions were normalized relative to the total theta, beta, and alpha power of all conditions, yielding a ratio (Mückschel et al., 2016):

$$\text{ratio} = \frac{\text{power}_{\text{3comp}} - \text{power}_{\text{0comp}}}{\text{power}_{\text{3comp}} + \text{power}_{\text{0comp}}}$$

Afterwards, clusters of activity differences in the alpha, beta, and theta frequency bands were identified between the response repetition and alternation conditions, in conjunction with the respective feature overlap levels. This was accomplished by implementing the Density-Based Spatial Clustering of Applications with Noise (DBSCAN) algorithm (Ester et al., 1996) using MATLAB. The clustering was performed based on the feature overlap cost ratio. This procedure, successfully employed in prior research (Prochnow et al., 2022; Wendiggensen et al., 2022; Adelhöfer and Beste, 2020; Adelhöfer et al., 2020), facilitated a focused analysis within distinct functional neuroanatomical regions. Depending on the direction of the significance testing effects at the sensor level, the upper or lower 1 % of the power distribution in the feature overlap cost ratio within labeled regions of the automated anatomical labeling atlas (Tzourio-Mazoyer et al., 2002) were subjected to DBSCAN. This allowed for a selection of voxels demonstrating the most significant negative or positive differences between the full and non-feature overlap conditions. An epsilon, set at 1.5 times the edge length of each voxel, was employed to identify neighboring voxels. Subsequent analyses were confined to these ROIs.

In step two, we utilized a Linear Constraint Minimum Variance beamformer to map out the timeline of source activity in the specified ROIs. From the averaged data's covariance matrix for each condition, we produced a spatial filter for each cluster of overlap minus no overlap cost-related activity. Afterwards this filter was multiplied with the pre-processed segmented data. Time-frequency analyses were conducted using Morlet wavelets (as described previously). The resulting power values were averaged across virtual channels (i.e., voxels) within each cluster, yielding a single time-frequency spectrum for each chosen ROI/functional neuroanatomical region. The feature overlap effect in the alpha, beta, and theta frequency bands was quantified by subtracting the non-overlap condition from the overlap condition.

Finally, Pearson correlations were performed across all time points within the pre-probe interval and all time-points in the within trial interval. The resulting correlation matrices underwent  $p$ -value adjustment applying the Benjamini-Hochberg method (Benjamini and Hochberg, 1995) to control for potential false positive findings. The corrected  $p$ -values, referred to as  $q$ -values, were used to determine significant correlations, which were further confined to a threshold of  $q < 0.05$ .

## 2.5. Statistical analysis of behavioral data

The analysis was conducted using JASP 0.16.4. The mean accuracy (percentage of correct responses) and the mean reaction time (in milliseconds) data (pertaining to correct responses) were computed for each

participant and condition. To evaluate binding effects, a repeated measures ANOVA was applied with the factors “response type” (response repetition or response alternation) and “feature compatibility” (no feature overlap or full feature overlap) as within-subject factors. In the following, mean values (mean) and standard deviations (SD) are reported in parentheses.

## 3. Results

### 3.1. Behavioral data

The behavioral data are shown in Fig. 3.

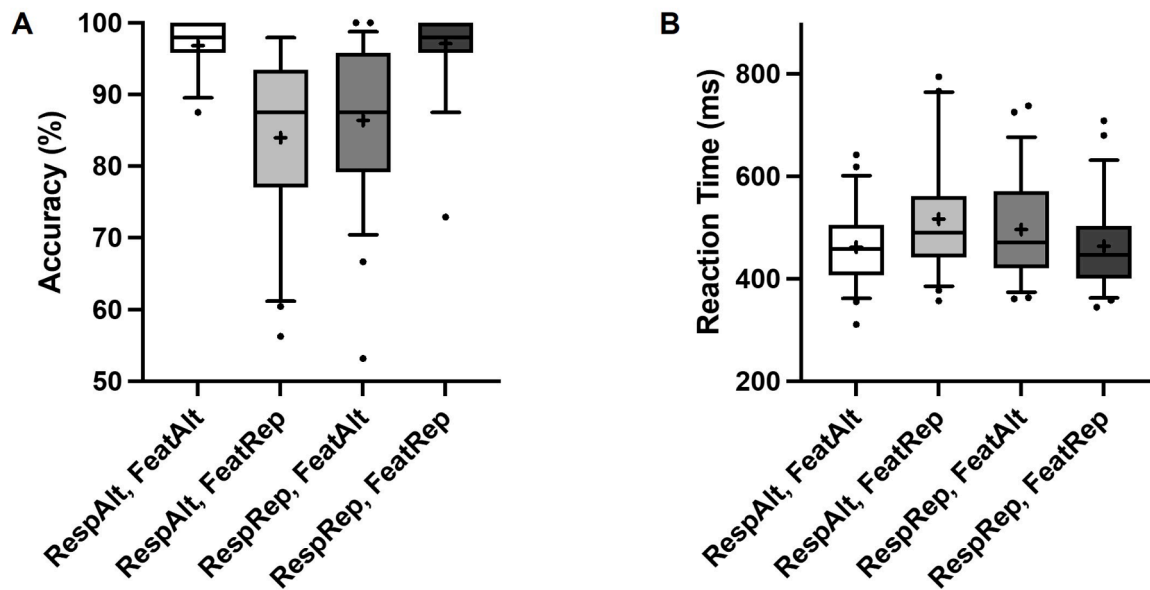
The repeated measures ANOVA with the factors feature overlap (full vs. no feature overlap), and response type (i.e. repetition or alternation) on the accuracy data showed no significant main effect of feature overlap [ $F(1,50) = 2.95, p = .092$ , partial  $\eta^2 = 0.056$ ], and response type [ $F(1,50) = 2.77, p = .103$ , partial  $\eta^2 = 0.052$ ]. However, the interaction of Feature overlap x Response type was significant [ $F(1,50) = 103.1, p < 0.001$ , partial  $\eta^2 = 0.673$ ]. Bonferroni corrected post hoc testing revealed that in case of response repetition, accuracy was significantly higher in the full feature overlap ( $M = 97.1\%$ ,  $SD = 4.78$ ) compared to the no feature overlap condition ( $M = 86.4\%$ ,  $SD = 9.7$ ,  $t(50) = -8.14, p < .001$ ). For the response alternation condition, a decrease of accuracy from the no overlap ( $M = 96.8\%$ ,  $SD = 3.37$ ) to the full overlap ( $M = 83.99\%$ ,  $SD = 11.83$ ,  $t(50) = 9.76, p < .001$ ) condition could be observed.

Regarding reaction times, the repeated measures ANOVA with the factors feature overlap (full vs. no feature overlap, and response type (i.e. repetition/alternation) showed a significant main effect of response type [ $F(1,50) = 6.7, p = .011$ , partial  $\eta^2 = 0.123$ ] and feature overlap [ $F(1,50) = 9.56, p = .003$ , partial  $\eta^2 = 0.161$ ] as well as a significant feature overlap x response interaction [ $F(1,50) = 80.46, p < .001$ , partial  $\eta^2 = 0.62$ ]. Bonferroni corrected post hoc testing showed that when a response had to be repeated, reactions were slower in the no feature overlap ( $M = 497$  ms,  $SD = 92$  ms) than in the full feature overlap ( $M = 464$  ms,  $SD = 80$  ms,  $t(50) = 5.34, p < .001$ ) condition. If an alternation of the response was required, reaction times were higher in case of full ( $M = 517$  ms,  $SD = 102$  ms) compared to the no feature overlap condition ( $M = 462$  ms,  $SD = 73$  ms,  $t(50) = 9.056, p < .001$ ). The behavioral results indicate that binding processes have taken place as binding is typically indicated by interaction effects (Hommel, 2004, 2009). Response repetition leads to lower accuracy rates and higher reaction times if the stimulus properties of S2 differ from those of S1. In this case, the pre-existing event file encompassing S1 (orientation, colour, position of the bar) and R1 (left or right key press according to the direction of the cue) has to be reconfigured now including the divergent stimulus features of S2 (different orientation, colour, position of the bar as S1) plus R2 (same direction of the keypress as R1). If, on the other hand, a change of the response is required (keypress in the opposite direction as R1), higher response times and lower response accuracy rates will result if the stimulus features of S1 and S2 are the same, since here, too, a previously formed event file has to be reconfigured.

### 3.2. Neurophysiological data

#### 3.2.1. Post-probe activity

In the first step, statistical analyses were conducted on the electrode level to establish whether significant differences between the conditions justified the subsequent beamforming analyses for the post-probe interval. In the repetition condition, FDR-corrected  $t$ -tests between the overlapping and non-overlapping condition revealed significant positive TBA differences during the post-probe interval (0 to 1 s relative to the onset of S2). The differences were significant ( $p > .05$ ) in the time frame between ~600 and ~700 ms. Additionally, significant negative power differences (non-overlap > overlap) were evident in the time frame from



**Fig. 3.** Behavioral Data. Box plots (A) for the mean accuracy (percentage of correct trials) and (B) the mean reaction times (for correct responses to S2). The four conditions are derived from the combination of response alternatives (Response Repetition = RespRep and Response alternation = RespAlt) and the feature overlap levels (Full feature overlap = FeatRep and no feature overlap = FeatAlt).

~50 to ~275 ms at parietal electrode locations (Fig. 4).

Subsequently, and based on DICS beamforming, two clusters of positive TBA differences (overlap > non-overlap) activity were identified by the DBSCAN algorithm in the repetition condition on the source-level. One cluster consisted of occipital areas and the cuneus (BA 17/18) while the other cluster encompassed right-hemispheric temporal and postcentral areas as well as the rolandic operculum (BA 41/B43; Fig. 4). Additionally, one cluster of negative TBA differences (overlap < non-overlap) was located in the left- and right-hemispheric Supplementary Motor Area (SMA; BA 6). In the alternation condition, significant differences in TBA between the overlap and non-overlap condition were evident across various electrode locations, most notably central-parietal areas. Positive differences (overlap > non-overlap) were observed around both before and after the approximate average RT. Beamforming and subsequent DBSCAN analysis revealed one cluster of postcentral TBA (BA 3/4) and one superior frontal/SMA cluster (BA 6/8). The identified clusters are used as regions of interest in subsequent analyses.

In the alpha frequency band, FDR-corrected *t*-tests revealed significant differences on single electrodes in both the repetition and alternation condition in the post-probe interval. However, activity in the alpha band in the probe interval was not source-reconstructed, as there was no coherent pattern in significance testing.

In the beta frequency band, significant differences on the electrode-level were found between the overlap and non-overlap condition in the repetition condition only. Significant positive differences (overlap > non-overlap) were evident in the time frame from ~300 to ~400 ms post-probe at occipito-parietal electrode locations. The DBSCAN algorithm revealed a cluster consisting of precentral and superior frontal regions (BA 6/8; Fig. 5) based on the DICS beamformed (source-reconstructed) data.

### 3.2.2. Pre-probe activity

Importantly, the time frame before the onset of the probe (S2) cannot be attributed to the individual conditions and can, therefore, not be contrasted between conditions. A statistical comparison on the sensor-level is usually used to justify the subsequent beamforming analyses (Pscherer et al., 2023; Wendiggensen et al., 2022), as applied for the post-probe interval in the current study. However, since the correlations are on the source-reconstructed time-courses based on the original time-series, any signal in the electrode level time series should also be

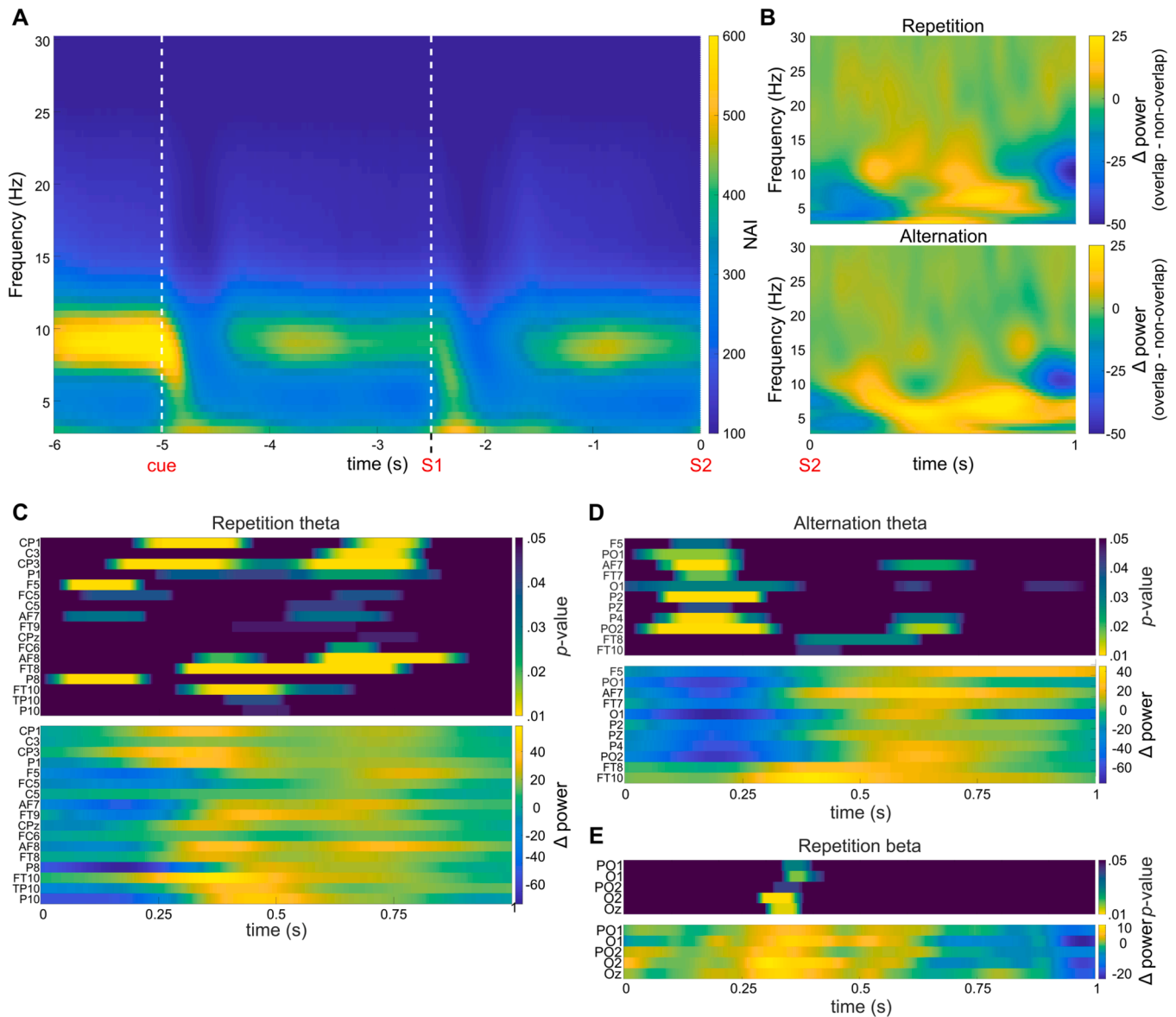
evident in the LCMV time series (Pscherer et al., 2023; Wendiggensen et al., 2022). If the signal was random, correlations in the LCMV data would be spurious and would not withstand FDR correction. The applied methodology therefore validates the clusters identified for the pre-probe time frames (Pscherer et al., 2023; Wendiggensen et al., 2022). For all three frequency ranges, the clustered 1 % of the strongest voxels revealed a similar area for all pre-probe time frames. The shape of the clusters varied slightly across time frames (i.e., pre-Cue, pre-S1, post-S1 and pre-S2) and between frequencies, but commonly encompassed areas in inferior frontal cortex, the insula and the superior temporal cortex (BA 38/44/45; see Fig. 5).

### 3.3. Correlation analyses

The source-reconstructed time series (i.e., the LCMV beamformed data) of each identified cluster were correlated between the pre-probe timeframes and the post-probe time period. Only significant correlations after FDR correction are reported. An overview of the significant correlations in the different frequency band (theta, alpha, beta) for the distinct phases of the experiment can be found in Table 1.

It is notable that significant associations between the clusters in the pre-probe time frames and the post-probe clusters were only evident for the repetition condition. There was no association between any of the pre-Cue, pre-S1, post-S1 and pre-S1 clusters and the post-probe binding effect in the alternation condition. The correlation matrices are visualized in Figs. 6 and 7. The theta activity pre-S1 cluster over the entire time frame correlated with the post-probe parieto-temporal theta activity cluster in the time frame from ~250 to ~450 ms ( $r_{max} = 0.54$ ;  $r_{min} = 0.36$ ;  $r_{mean} = 0.46$ , within area  $q < 0.05$ ). This indicates a positive association between TBA in the pre-S1 cluster and the post-probe TBA-associated overlap effect. A similar association was found between the post-probe parieto-temporal theta activity and TBA clusters in the post-S1 ( $r_{max} = 0.55$ ;  $r_{min} = 0.36$ ;  $r_{mean} = 0.47$ , within area  $q < 0.05$ ) and pre-S2 ( $r_{max} = 0.55$ ;  $r_{min} = 0.36$ ;  $r_{mean} = 0.48$ , within area  $q < 0.05$ ) intervals, where higher TBA over the entire time interval pre-probe was related to a higher post probe TBA-associated overlap effect in the time frame from ~250 to ~450 ms.

For ABA, the clusters in the pre-S1, post-S1 and pre-S2 correlated significantly with the parieto-temporal TBA cluster in the time period from ~250 to ~450 ms over the entire respective one second time



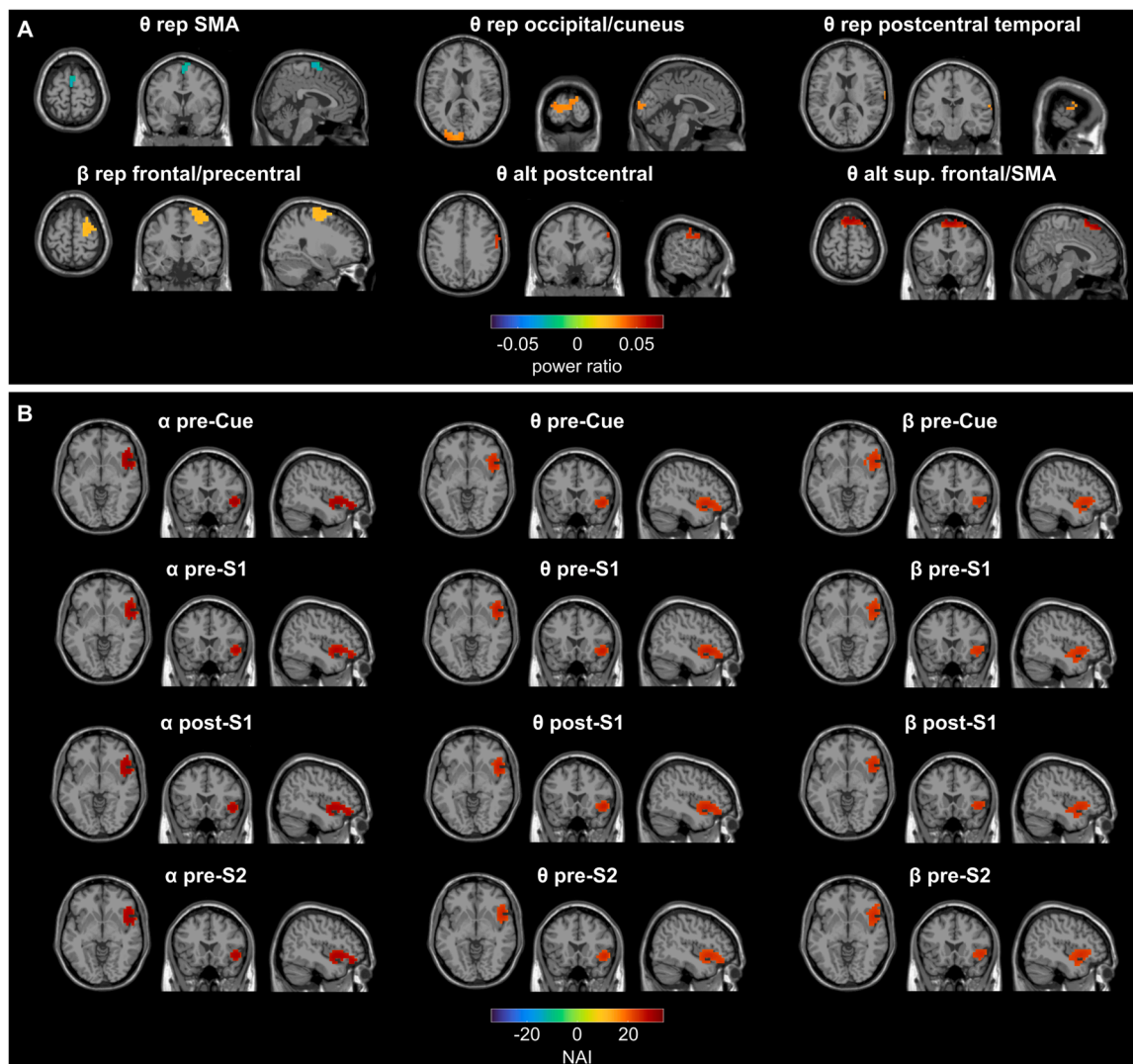
**Fig. 4.** Neurophysiological results on the sensor-level. **A** Time-frequency representation of the pre-probe period. The time is given relative to the onset of S2, the color scales the magnitude of the Neural Activity Index (NAI). **B** Time frequency decomposition for the post-probe interval in repetition (top) and alternation (bottom) trials. The colorbar represents the difference between the overlap and non-overlap condition. **C-E** Significant time frames in the FDR corrected  $t$ -tests. The top plot shows the  $p$ -values for channels (y-axis) and time, the bottom plot shows the power difference (overlapping – non-overlapping).

period. This relationship was (mostly) positive, indicating that higher alpha band activity in the pre-S1 ( $r_{max} = 0.51$ ;  $r_{min} = 0.42$ ;  $r_{mean} = 0.46$ , within area  $q < 0.05$ ), post-S1 ( $r_{max} = 0.55$ ;  $r_{min} = 0.36$ ;  $r_{mean} = 0.42$ , within area  $q < 0.05$ ) and pre-S2 ( $r_{max} = 0.55$ ;  $r_{min} = 0.34$ ;  $r_{mean} = 0.34$ , within area  $q < 0.05$ ) period was related to a higher TBA overlap effect in the post-probe period. For pre-probe BBA, only the pre-S2 cluster was positively correlated over with the TBA related overlap effect in the post-probe interval ( $r_{max} = 0.49$ ;  $r_{min} = 0.36$ ;  $r_{mean} = 0.41$ , within area  $q < 0.05$ ). The correlation was significant from  $\sim 300$  to  $\sim 450$  ms post probe across the entire pre-S2 timeframe.

Furthermore, there were significant correlations between the post-probe occipital cuneus TBA cluster and the pre-probe ABA and BBA clusters in the pre-probe time frames (Fig. 7). ABA in the pre-Cue, pre-S1, post-S1 and pre-S2 cluster over the entire time frame was positively related to the TBA related overlap effect in the occipital/cuneus cluster in the time frame between  $\sim 500$  and  $\sim 800$  ms (relative to probe onset). The correlation coefficients within the significant area  $q < 0.05$  ranged from  $r_{min} = 0.34$  to  $r_{max} = 0.50$  with consistent average correlation

coefficients for each correlation matrix (see Table 1). The results indicate that higher ABA before probe-onset was related to a higher TBA associated overlap effect in the cuneus/occipital cortex cluster or vice versa. Likewise, also BBA pre-probe was positively correlated with the post-probe TBA cuneus/occipital cortex cluster. The correlations were significant across the entire one second time window for each pre-probe time frame and between  $\sim 500$  and  $\sim 800$  ms on the post-probe time axis. Although the average correlation coefficients are approximately equal across time frames, the coefficients generally lowest in the pre-Cue time frame ( $r_{max} = 0.46$ ) and highest in the post-S1 time window ( $r_{max} = 0.56$ ). The correlations indicate that higher BBA pre-probe is associated with a higher TBA associated overlap effect in the cuneus/occipital cortex cluster.

The clusters in all pre-probe time frames (i.e., the spatially overlapping clusters in inferior frontal cortex, the insula and the superior temporal cortex during pre-Cue, pre-S1, post-S1, and pre-S2) were significantly correlated with each other at each time point between the frequency bands (i.e., theta, alpha and beta); all  $q < 0.001$ . The mean



**Fig. 5.** Clusters of activity as identified by the DBSCAN algorithm. **A** Clusters identified for the within trial interval on the source reconstructed EEG data. The color of the voxels scales the power ration (overlap – non-overlap / overlap + non-overlap). In the labels, “alt” and “rep” are abbreviations for the alternation and repetition condition, respectively. **B** Clusters identified in the pre-probe intervals where the frequency bands are used as columns and rows for the different time-intervals.

**Table 1**

Mean r-values within significant area  $q < 0.05$  for each correlation matrix. The columns indicate the respective time frames while the rows represent the clusters of ABA, BBA and TBA. Mean correlation values between frequency band activity in the pre-probe intervals and TBA in the two post-probe clusters are provided for correlation matrices with significant areas in the respective time frames (last column).

	pre Cue	pre S1	post S1	pre S2	post S2
$\alpha$	–	.42	.46	.34	~250 – 470 ms
$\beta$	–	–	–	.41	postcentral/ temporal
$\theta$	.42	.46	.47	.48	~480 – 720 ms
$\alpha$	.41	.43	.43	.42	occipital/ cuneus
$\beta$	.41	.43	.45	.43	
$\theta$	–	–	–	–	

correlation coefficients for the individual correlation matrices ranged from  $r_{min} = 0.78$  to  $r_{max} = 0.98$ .

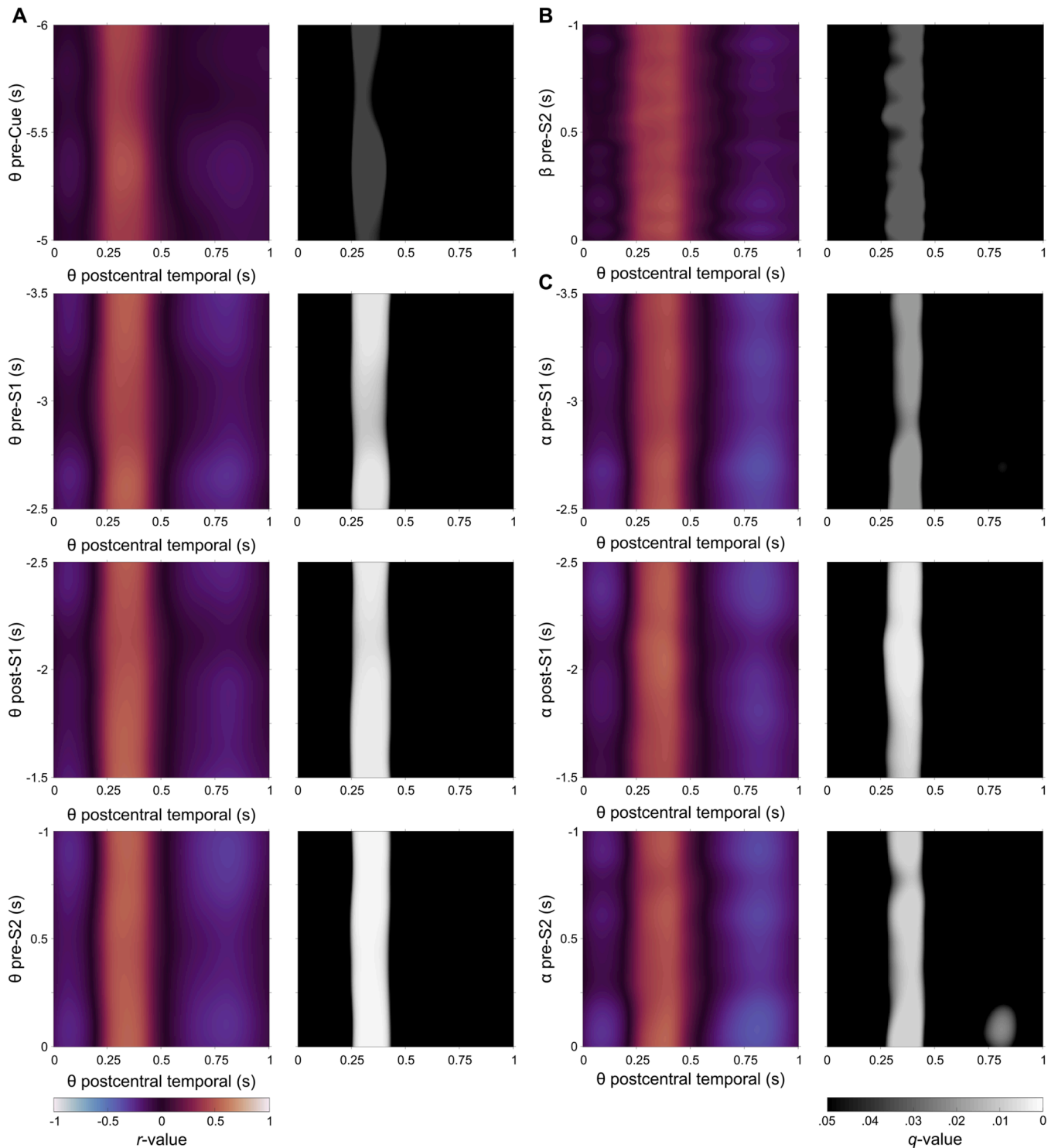
#### 4. Discussion

The current study examined the neurophysiological principles

underlying the dynamic management of integrated perception-action bindings. While research in cognitive neuroscience has long been examining the neural correlates of goal-directed behavior, these analyses were mostly restricted to specific parts of experimental data – that is parts where some (stimulus) information requires a response according to a specific rule. However, as more recently framed in the BRAC framework, such an analysis falls short because it does not consider that human action control is reliant on the “immediate past” of what has been processed in the sensorimotor system (Beste et al., 2023; Frings et al., 2020). To examine this in more detail, the current study took advantage of an experimental design (Colzato et al., 2006), in which goal-directed responses depend on the acquisition of multiple stimulus-response associations in their immediate history. Across distinct phases of the experiment, TBA, ABA and BBA was examined and inter-related across the different phases of the experiment.

The behavioral data obtained is in line with previous studies using this task (Colzato et al., 2006) documenting an interaction of stimulus and response features that indicates a binding of these aspects (Hommel, 2004, 2009); i.e., an integration of stimulus and response features in a common representational format (the event file). The neurophysiological data analysis in the different frequency bands revealed event



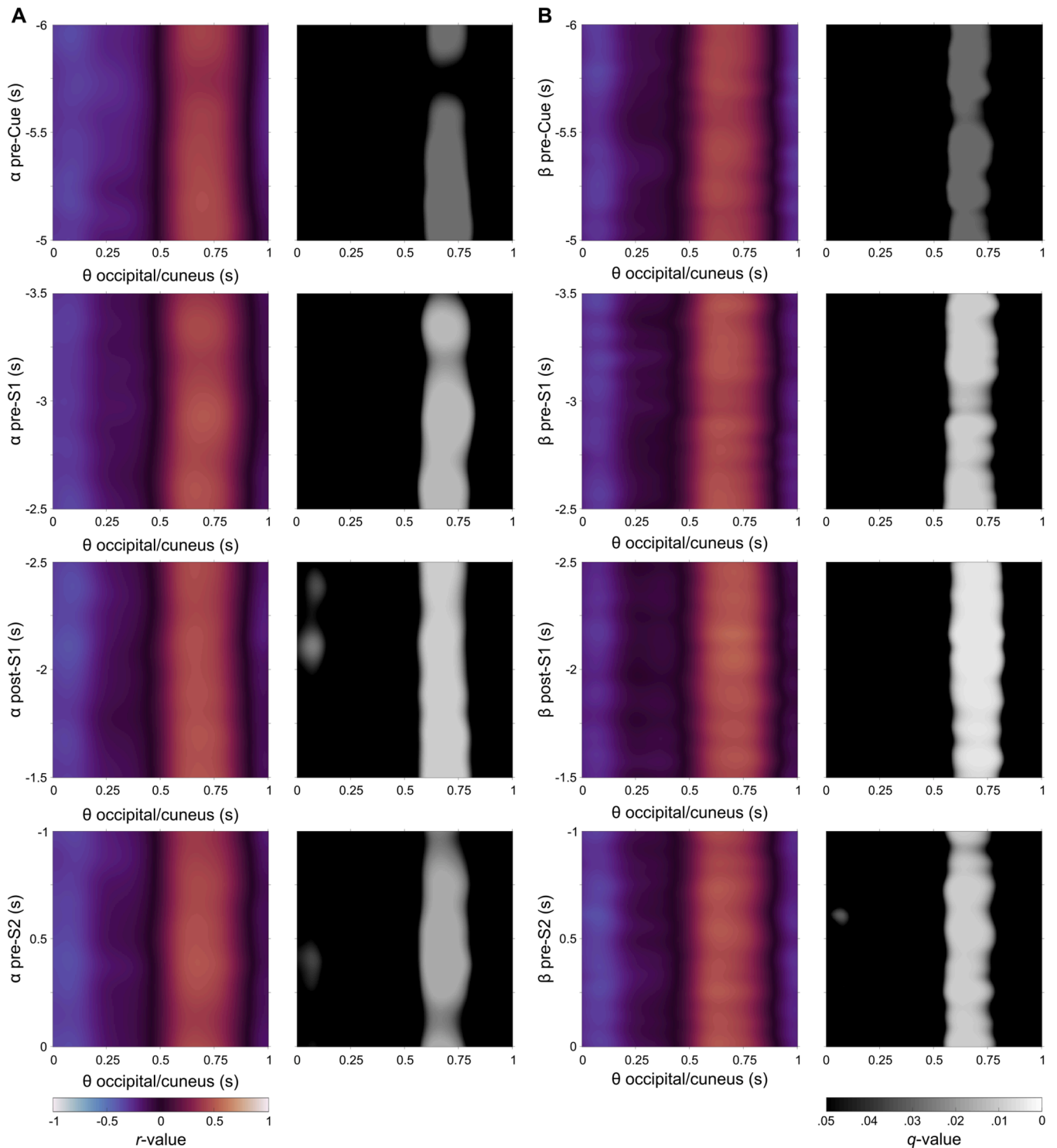


**Fig. 6.** Correlations between the postcentral/temporal TBA cluster (always on the x-axis) and the pre-probe clusters. Please note that only significant correlations are shown. The left plot always represents the correlation matrix (correlation coefficient scaled by color) while the right plot depicts the  $q$ -value (FDR-corrected  $r$ -values; black areas are non-significant). The different pre-probe clusters are indicated on the y-axis: **A** pre-probe TBA clusters, **B** BBA in the pre-S2 interval, **C** pre-probe ABA clusters.

file binding effects (i.e., processes examined after the S2 (probe) stimulus). In accordance with our hypotheses, TBA appears to be notably linked to retrieval processes. Considering the repetition condition, reconfiguration is required whenever stimulus features change (no feature overlap). In the response alternation condition, however, a reconfiguration of the event file is necessary when stimulus characteristics remain constant (full feature overlap). Our results revealed a

modulation of TBA shortly after the appearance of the probe stimulus such that TBA was increased in the condition where reconfiguration was required, as compared to trials where the established event file could be maintained. This is in line with previous studies (Prochnow et al., 2022; Takacs et al., 2020b).

The correlational analyses between the pre-probe clusters in the different frequency bands revealed high correlations between the



**Fig. 7.** Correlations between the occipital/cuneus TBA cluster (always on the x-axis) and the pre-probe clusters. Only correlation matrices with significant areas are shown. The left plot always scales the magnitude of the correlation coefficients while the right plot depicts areas of significance. The different pre-probe clusters are indicated on the y-axis: **A** pre-probe ABA clusters, **B** pre-probe BBA clusters. The pre-probe clusters are sorted by time, i.e., pre-Cue clusters in the top row are furthest from S2 onset while pre-S2 clusters in the last row are closest.

overlapping regions. This is in line with previous studies, where pre-trial activations in different frequencies but overlapping sources were associated with each other (Pscherer et al., 2023).

#### 4.1. Impact of the immediate history on dynamic event file management

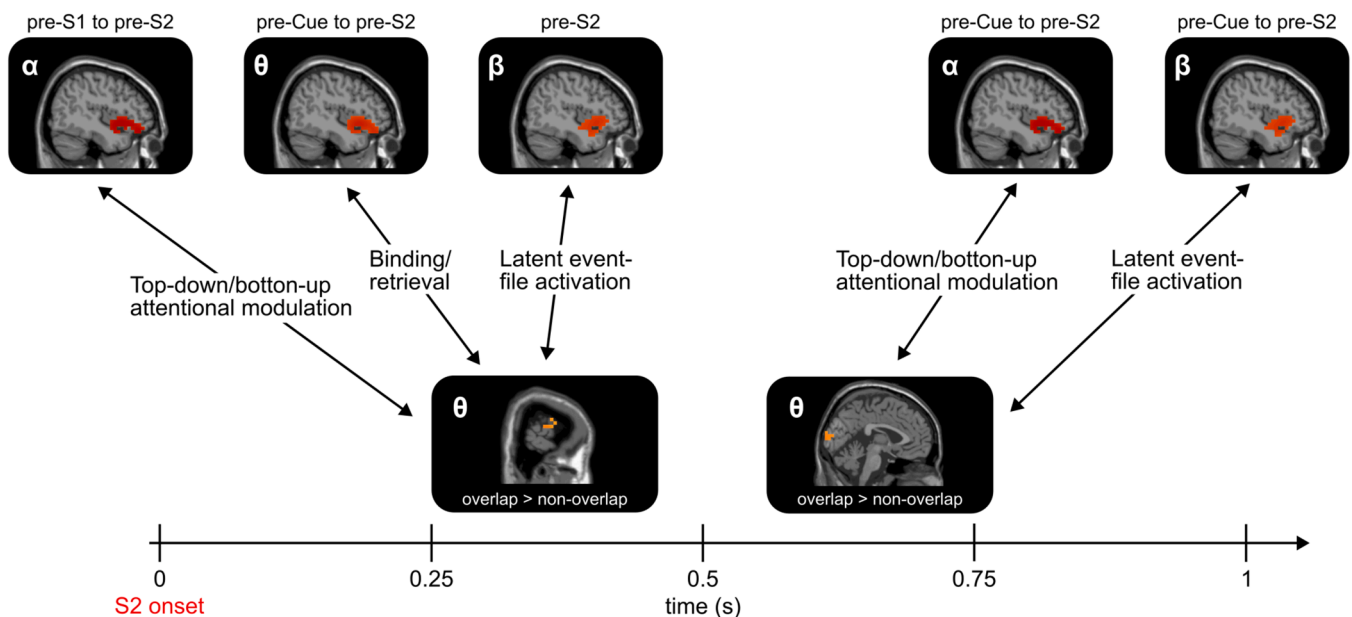
However, most important for the focus of the current study is the

pattern of the correlation analysis. At present, the conceptual framework (Beste et al., 2023; Frings et al., 2020) does not distinguish between response repetition and alternation as regards the underlying neural processes. The event file can be conceived as building the connections/associations between stimulus features and motor features (Hommel, 2004) and it has been assumed that event file dynamics are the same in response repetition and alternation trials depending on

whether a reconfiguration of the event file as indicated by stimulus input is necessary (Hommel, 2004, 2009). While this may still be the case during the retrieval of an event file (i.e., after the probe stimulus, S2), the data show that there is an asymmetry in the inter-dependence of neural processes relying on the immediate past, which is a conceptual novelty: significant associations between the clusters in the pre-probe time frames and the post-probe clusters were only evident for the response repetition condition. This suggests that the immediate past has an impact particularly when no changes in the configuration of features determining the motor part of an event file are required. It seems that particularly the reconfiguration process of the motor parts of the event file at the time of event file retrieval (i.e., after the probe (S2) stimulus) over-writes the immediate past, which otherwise has a strong impact during event file retrieval. The pattern of the correlational results showing an impact of the immediate past on event file retrieval is summarized in Fig. 8. The following discussion is organized such that first, the correlational pattern with TBA-related event file retrieval processes in the time interval up to 500 ms after presentation of the S2 is discussed. Then, we discuss the findings on the correlation analysis from 500 ms onwards. It is important to consider that conclusions about associated locations should only be interpreted with caution due to the limited number of (60) electrodes used in this study. However, using a large number of participants, this was accounted for.

As shown in Fig. 8, inferior frontal cortex, insula and the superior temporal cortex (BA 38/44/45) activity in the TBA, ABA and BBA correlated positively with activity early on (i.e., within the first ~450 ms) during processing the probe in the theta frequency band in temporal and postcentral areas and the rolandic operculum (BA 41/43). It has been suggested that TBA is involved in the retrieval of an event file (Beste et al., 2023). In keeping with a previous study, TBA was modulated early on after the probe stimulus was presented (Takacs et al., 2020a). Interestingly, especially ABA was most consistently correlated with event file retrieval-related TBA, since correlations were evident for the pre-S1 phase, post-S1 and the pre-S2 phase. This suggests a more overarching process of ABA during all phases of the experiment. It has been proposed that within the BRAC-framework, ABA likely reflects top-down and bottom-up attentional modulation of binding and retrieval processes, which is in line with the well-established conception of inhibitory gating processes exerted by ABA (Klimesch, 2012). ABA is

important to guide the selection of relevant features and discarding of irrelevant features for goal-directed behavior and may thus crucially coordinate binding and retrieval dynamics of event files (Beste et al., 2023). Taking this perspective, it is reasonable that ABA is correlated with retrieval-related TBA. Furthermore, also the involvement of the identified brain regions is plausible since these functions have been associated with these regions (Bedini and Baldauf, 2021; Cai et al., 2016; Higo et al., 2011; Nelissen et al., 2013; Tsumura et al., 2022). The same regions that were shown to be associated with ABA, were also associated with pre-S1 and pre-S2 TBA and retrieval-related TBA after the presentation of the S2 stimulus. This pattern is well in line with recent neurophysiological framings of BRAC (Beste et al., 2023), according to which TBA is involved in the binding and the retrieval process of an event file. According to BRAC, binding and retrieval processes are both involved whenever a stimulus comes up and a response has to be executed (Frings et al., 2020). Information of the S1 stimulus and the response to the cue becomes associated shortly after the presentation of the S1 stimulus that is retrieved upon the presentation of the S2 stimulus. Binding and retrieval processes are both mediated via TBA. However, during binding (i.e., pre-S1 and pre-S2), adjacent (insular), but also different functional neuroanatomical structures (inferior frontal cortex, superior temporal cortex) play a role. Insular cortex areas have supra-modal properties and are well-known to perform sensorimotor integration (Evrard, 2019; Gogolla, 2017). More recently, these have also been brought into connection with event file dynamics (Gholami-pourbarogh et al., 2023). Besides their role in top-down control processes discussed above, the inferior frontal cortex and the superior temporal cortex also play a role for the processing of sensorimotor features for purposeful actions (Borra et al., 2017). Since the anterior part of the temporal cortex is part of the ventral stream pathway involved in the processing of the identity of visual features (Chao and Martin, 1999; Goodale et al., 2005; Goodale and Milner, 1992), it is reasonable that these regions are also involved in the theta-related binding processes. The involvement of the ventral pathway during event file binding may reflect processing of the stimulus features, as shown before (Corbetta et al., 2008; Hampshire et al., 2010). The strong correlations between TBA during retrieval (i.e., post S2) and TBA relevant for event file binding (i.e., pre-S1, pre-S2) provide the first evidence directly supporting neural mechanistic principles of the BRAC framework (Beste



**Fig. 8.** Summary of the results. The observed correlational patterns are summarized in this figure. The time axis represents the post-probe time frame (i.e., after the onset of S2). In the top row, the pre-probe clusters are depicted exemplary for all pre-probe time intervals. Significant correlations between the pre-probe clusters and the post-probe clusters are highlighted in the time frame of significance on the time axis.

et al., 2023).

BBA prior the probe (S2) presentation was correlated with retrieval-related TBA. Some evidence suggests that BBA reflects the information of a just formed event file (Beste et al., 2023; Pastötter et al., 2021; Wendiggensen et al., 2022) – that is the maintenance of information in an event file. In the experimental approach used, the event file has been created/bound after the S1 stimulus. Therefore, meaningful BBA before the S1 stimulus that is correlated with retrieval processes after the S2 also corroborates assumptions of the neural processes supporting the dynamic management of event files as outlined in the BRAC framework.

500 ms after probe onset (cf. Fig. 8), the correlational pattern and the pattern of functional neuroanatomical structures related to TBA change: then, visual association cortices encompassing the cuneus were associated with TBA. Importantly, the behavioral data revealed that the participants on average responded within the first 500 ms. Therefore, TBA from 500 ms onwards cannot reflect processes that are part of the actual event file retrieval and response selection process. Instead, such TBA in visual areas likely reflects a preparation for potentially upcoming new information. Indeed, TBA plays a role in attentional control (Spyropoulos et al., 2018) and several lines of evidence suggest that information sampling (Fiebelkorn et al., 2013; Helfrich et al., 2018; Landau and Fries, 2012; Vanrullen and Dubois, 2011) for action control follows a theta rhythm (Wilken et al., 2023). Of note, ABA and BBA during all periods of the task analyzed (i.e., pre-cue, pre/post-S1, pre-S2) correlated with the cuneus cortex TBA. As mentioned above, ABA supports attentional control through inhibitory gating guiding the selection of relevant features and discarding of irrelevant features for goal-directed behavior (Klimesch, 2012). From that perspective it is possible that the obtained correlation could reflect an attentional sampling of features in potentially upcoming information that are relevant for goal-directed behavior. Arguing along these lines it is also reasonable that BBA was correlated given that it likely reflects the maintenance of relevant information in an event file that may be updated through the attentional sampling processes once response selection processes have been completed (i.e., retrieval-related TBA after 500 ms). At first sight, event file maintenance related BBA might be considered at odds with the finding that also pre-cue BBA was correlated, activity at a time when no event file has yet been created. It must be considered, though, that BBA has long been conceptualized as signaling the general status quo of the sensorimotor system (Engel and Fries, 2010). The conception of BBA within the BRAC-framework reflects a specification of this during time periods where specific associations between stimulus and response features have been built (Beste et al., 2023). Recent findings have already reported BBA in time phases of experiments analyzing the binding of motor features (Wendiggensen et al., 2022). Moreover, TBA and BBA are jointly involved in motor control (Herrmann et al., 2016; Singh et al., 2020).

Taken together, the correlations obtained suggest that once TBA-related event file retrieval processes are finished, the functional significance (together with the neuroanatomical implementation) changes reflecting processes relevant to prepare the cognitive system for upcoming demands. Future studies should place an emphasis on additional parameters, for example trial-to-trial variability. Due to possible interdependencies between trial  $n-1$  and trial  $n$ , this is not possible in the current experiment. The paradigm therefore would need to be adjusted to control for such trial transitions.

## 5. Conclusions

In summary, the present study provides novel insights into the neurophysiological mechanisms of event file dynamics. It was demonstrated for the first time that, interdependencies of neuronal processes relying on the immediate past occur. The reconfiguration of an action seems to overwrite immediately preceding processes. The analyses revealed modulations of TBA, ABA and BBA in connection with fronto-temporal structures supporting the theoretical assumptions of the BRAC

framework. The close interplay of attentional modulation by gating irrelevant information (ABA) and binding and retrieval processes (TBA) is reflected by the correlation of ABA in all pre-probe-intervals with post-probe TBA. Likewise, the role of BBA in maintaining the event file until retrieval is corroborated by BBA preceding the TBA-associated retrieval of perception-action codes. Following action execution, TBA shifted towards visual association cortices probably reflecting preparation for upcoming information, while ABA and BBA continue to reflect processes of attentional control and information selection for goal-directed behavior. Although the examined relationships constitute correlational analyses, thereby precluding causal inferences, the temporal sequencing of the findings suggests a causal association. The present work provides the first empirical support for concepts about the neurophysiological mechanisms of dynamic management of perception and action.

## CRedit authorship contribution statement

**Tina Rawish:** Formal analysis, Investigation, Visualization, Writing – original draft, Writing – review & editing. **Paul Wendiggensen:** Formal analysis, Methodology, Validation, Visualization, Writing – original draft, Writing – review & editing. **Julia Friedrich:** Conceptualization, Funding acquisition, Validation, Visualization, Writing – original draft, Writing – review & editing. **Christian Frings:** Conceptualization, Funding acquisition, Writing – review & editing. **Alexander Münchau:** Funding acquisition, Project administration, Validation, Writing – original draft, Writing – review & editing. **Christian Beste:** Conceptualization, Funding acquisition, Methodology, Project administration, Resources, Supervision, Validation, Writing – original draft, Writing – review & editing.

## Declaration of competing interest

There are no conflicts of interest.

## Data availability

Data will be made available on request.

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