



Research Report

The temporal dynamics of how the brain structures natural scenes



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ABSTRACT

Individuals organize the evolving stream of events in their environment by partitioning it into discrete units. Event segmentation theory (EST) provides a cognitive explanation for the process of this partitioning. Critically, the underlying time-resolved neural mechanisms are not understood, and thus a central conceptual aspect of how humans implement this central ability is missing. To gain better insight into the fundamental temporal dynamics of event segmentation, EEG oscillatory activity was measured while participants watched a narrative video and partitioned the movie into meaningful segments. Using EEG beamforming methods, we show that theta, alpha, and beta band activity in frontal, parietal, and occipital areas, as well as their interactions, reflect critical elements of the event segmentation process established by EST. In sum, we see a mechanistic temporal chain of processes that provides the neurophysiological basis for how the brain partitions and structures continuously evolving scenes and points to an integrated system that organizes the various subprocesses of event segmentation. This study thus integrates neurophysiology and cognitive theory to better understand how the human brain operates in rather variable and unpredictable situations. Therefore, it represents an important step toward studying neurophysiological dynamics in ecologically valid and naturalistic settings and, in doing so, addresses a critical gap in knowledge regarding the temporal dynamics of how the brain structures natural scenes.

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1. Introduction

In the face of complex, ongoing streams of events in our environment, agents likely organize “what is happening” around by segmenting dynamic scenes into discrete representational units (Franklin, Norman, Ranganath, Zacks, & Gershman, 2020; Richmond & Zacks, 2017; Zacks, 2020; Zacks, Speer, Swallow, Braver, & Reynolds, 2007), which in turn serve to orchestrate adaptive behavioral control. Event Segmentation Theory (EST) is the most comprehensive theoretical framework for capturing the processes involved in the building of discrete events on a cognitive level (Sargent et al., 2013; Zacks, Speer, & Reynolds, 2009): Aspects of “what is happening now” are integrated to a working event model, so the idea, which is supposed to work back on perceptual processes in a loop by biasing sensory processing, based on, and in concert with (top-down) modulations provided by long-lasting memory representations (i.e. event schemata) (Zacks & Sargent, 2010). These schemata result from previous experience and provide expectations based on world-knowledge about highly probable event sequences (e.g., a bus arriving while waiting on a bus stop). The working event model's performance to predict what is coming up next is evaluated by error detection mechanisms comparing the working event model's predictions to what actually happens. Whenever predictions fail, the representation of an event segment in working memory is closed and the representation of a new segment is opened.

While several fMRI studies have delineated neural dynamics related to the event segmentation processes in several brain regions, for instance, the lateral prefrontal cortex and the anterior cingulate cortex (Baldassano et al., 2017; Hasson, Nir, Levy, Fuhrmann, & Malach, 2004; Kurby & Zacks, 2008; Magliano & Zacks, 2011; Speer, Zacks, & Reynolds, 2007, 2009; Zacks et al., 2001, 2007, 2010), the temporal neural dynamics underlying event segmentation are largely contentious. This gap in research is a conceptual problem because the process of dissecting an ongoing stream of information into discrete segments is necessarily a process defined by temporal aspects (i.e., how a situation evolves). Related to this, it is neural oscillatory activity at different frequencies which reflects a fundamental principle of information processing in the brain (Beste, Münchau, & Frings, 2023; Buzsáki, Logothetis, & Singer, 2013; Varela, Lachaux, Rodriguez, & Martinerie, 2001) and which is also of relevance when it comes to the question of how information is being integrated (Engel & Singer, 2001; Singer, 2011). The fact that these processes in event segmentation have not yet been thoroughly investigated – although they are of conceptual relevance – is partly due to the difficulty of applying electrophysiological methods (e.g., EEG) developed and validated in artificial situations with predefined, clear-cut units/segments of interest (i.e., trials) to more variable and a priori unpredictable situations in which these units of interest are continuously defined by the person themselves (e.g., while watching a movie). In the current study we adapted EEG analysis methods to enable a conceptually meaningful examination of oscillatory activity during movie scene comprehension and segmentation. This provides an important step towards a more ecologically valid neurophysiology of higher-level cognitive

processes and towards a mechanistic understanding of how the human brain organizes the continuous stream of events happening around us.

According to the EST, important components of the event segmentation process are the *working event model*, which refers to the currently active representation of the situation, and the *event schema*, which refers to the long-term representation of how similar situations or events normally proceed (Zacks, 2020; Zacks et al., 2007; Zacks & Sargent, 2010). Alpha band activity (ABA) is thought to mainly reflect the inhibitory gating mechanisms controlling access of information to a long-term “knowledge system” and working memory (Klimesch, 2011, 2012; Klimesch, Sauseng, & Hanslmayr, 2007; Roux & Uhlhaas, 2014). Since long-term knowledge and event schemata share conceptual similarities, one central mechanistic element in the way the brain structures natural scenes, may be reflected in ABA. Furthermore, the EST supposes the monitoring and updating of working event models (Zacks & Sargent, 2010), in the sense that the current status of the environment in relation to individuals' goals and assumptions about the world around them is continuously evaluated. Monitoring, maintaining, and updating the expected “status quo” is likely reflected in beta band activity (BBA) (Engel & Fries, 2010; Jenkinson & Brown, 2011; Spitzer & Haegens, 2017), as is an endogenously controlled transfer of latent memory content into current working memory (Spitzer & Haegens, 2017). Both aspects are relevant considering the role of working event models and their interplay with event schemata in the EST, which is why besides ABA, also BBA may be relevant in how the brain structures natural scenes. Moreover, ABA and BBA may show close inter-relations, because the control of access of information stored in a “knowledge system” (cf. ABA) and the monitoring of status quo as well as the transfer of information between memory systems (cf. BBA) show close conceptual inter-dependencies. Another central assumption of EST is that boundaries between successive event segments are set whenever predictions based on the current working event model fail (Zacks et al., 2007; Zacks & Sargent, 2010). Such signaling has been ascribed to theta band activity (TBA) modulations (Cavanagh, Frank, Klein, & Allen, 2010, 2012; Cavanagh & Frank, 2014), which is also important during attentional sampling of the environment (Busch & VanRullen, 2010; Fiebelkorn et al., 2013; Kienitz et al., 2018; Landau & Fries, 2012; Spyropoulos, Bosman, & Fries, 2018; VanRullen & Dubois, 2011; VanRullen, Carlson, & Cavanagh, 2007; Wendiggen, Ghin, Koyun, Stock, & Beste, 2022). Therefore, TBA may be a third mechanistic element. All three elements, TBA, ABA and BBA, may show inter-relations or a mechanistic chaining of processes. As these three frequency bands reflect the mechanistic elements described in the EST, there are no hypotheses and thus no analyses on any other frequency bands.

2. Material and methods

We report how we determined our sample size, all data exclusions, all inclusion/exclusion criteria, whether inclusion/exclusion criteria were established prior to data analysis, all manipulations, and all measures in the study.

2.1. Participants

The study included $N = 34$ young healthy individuals, ranging in age from 18 to 30 years. $N = 4$ individuals had to be discarded to due problems in data recording. The final analyses thus included data from 30 individuals (13 females and 17 males, mean age 25.43 ± 2.95 years). Considering previous studies on event segmentation (Eisenberg, Zacks, & Flores, 2018; Kurby & Zacks, 2011; Zacks et al., 2009, 2010) and EEG studies (Bensmann, Zink, Werner, Beste, & Stock, 2020; Guttmann-Flury, Sheng, Zhang, & Zhu, 2019; Hong, Sun, Wang, Li, & Tong, 2020; Takacs & Beste, 2023), this number of participants should be sufficient to analyze event segmentation and related neurophysiological processes. Participants were recruited through the University Clinic Carl Gustav Carus and the Technical University of Dresden's database as well as advertisements. Participants were screened prior to participation to ensure that they had no history of neurological or psychiatric disorder, normal or corrected-to-normal vision, no chronic or acute medication, and no history of substance abuse or dependence. At the time of the experiment, participants provided written informed consent and were compensated for their participation with 10 EUR. The local ethics committee of the Medical Faculty of the Technical University of Dresden approved the study. No part of the study procedures and analyses have been preregistered.

2.2. Task

Participants started the experiment with a practice session. The practice video clip presented a man assembling a boat using “Duplo” construction blocks (Zacks et al., 2009). Participants were instructed to segment the movie by pressing the space button to indicate the time that they perceived something (e.g., action, behavior, interaction) was ending or something in the movie was about to start. It was stated in the instruction as well that there is no right or wrong answer and only their individual assessment is important. Following the practice session, participants watched the well-established movie “The Red Balloon” [Lamoris & (Director), 1956, October 19] and at the same time the EEG was recorded. In the movie “The Red Balloon” the relationship of a little boy and a balloon who become friends is depicted. This movie has several specific characteristics that make it suitable for examining event segmentation, such as a small amount of spoken language, frequent situational changes, and nearly no jumps in time (Magliano & Zacks, 2011; Zacks et al., 2009, 2010). The film was divided into four 7–10 min episodes (lengths of 463.3, 468.4, 446.2, and 600.6 sec); with pauses in between each clip (Zacks et al., 2009). By tapping the space button, participants were able to resume the task. All of the videos were shown using the “Presentation” software (NeuroBehavioral Systems Inc.). Different from the previous study (Zacks et al., 2009), the participants did not watch the movie a second time without pressing any keys, as task compliance could not have been ensured in this case and the data could thus neither be evaluated as event-related nor as resting-state. Also, no motor control condition such as free key pressing was implemented, as here no examination of possible internal rules/strategies of the participants would

have been possible. Thus, in both cases, the obtained data would have been hardly analyzable.

Situational changes in each video clip of “The Red Balloon” had already been specified and scored frame by frame for nine types of situational changes during the study by Zacks et al. (2009) and has been validated in their study. Therefore, this established rating scheme was also applied in the current study. The documentation of the situational changes, the code and stimuli of the paradigm as well as the behavioral and neurophysiological data of the study have been deposited under the following link: <https://osf.io/zsfx8/>

The changes are characterized as follows: (i) “Character change” when the focus of the action was an animate character or characters, and this emphasis was changed from the previous frame. (ii) “Character-character change”, which was referring to the interactions, such as touching, conversing, gesturing, or coming together while walking or running. It thus reflects alterations in the physical or abstract interactions between characters. (iii) “Character-object change”, described as the time a character's interaction with an object changed, such as the time they picked up an object or started using an object they already had in a new way. (iv) “Temporal change” was happening when a frame was temporally discontinuous from the frame before. (v) “Large Space change” and (vi) “Small Space change” reflect a location change of the character from the previous scene to the next one or changes in the narrative point of view regarding the level of the shots, respectively. (vii) “Cause changes”, which occurred when the activity in a frame could not be justified by something seen in the previous frame. (viii) “Goal change” is coded as the time at which a film character took an action connected with a goal different from the one in the previous frame. The last change was characterized as a (ix) “Scene change”, which referred to the time that a whole shot changed to a new one. For the behavioral analysis, each clip in the movie was divided into intervals of 2 sec (982 intervals in total), which is in line with previous studies (Zacks et al., 2009). The intervals were either categorized as Boundary interval, if a button press marked an event boundary occurred in it, or as No-Boundary interval, if no button press occurred in it. Further, the changes per interval were counted, both collectively and separately by change type.

2.3. EEG recording and pre-processing

EEG signals were recorded from 60 Ag/AgCl electrodes at equidistant scalp positions (reference electrode at FPz, ground electrode at $\theta = 58$, $\phi = 78$) mounted in an elastic cap (EasyCap Inc.) while participants were watching the movie. The EEG was recorded using a BrainAmp amplifier (Brain Products Inc.). The sampling rate was at 500 Hz, which was then down-sampled offline to 300 Hz in order to align the sampling rate of the EEG data with the frame rate of the presented movie (30 Hz). The electrode impedances were kept under 5 k Ω . The “Automagic” pipeline (Pedroni, Bahreini, & Langer, 2019) and EEGLAB (Delorme & Makeig, 2004) running on MATLAB 2019a (The MathWorks Corp) were used for EEG pre-processing. Flat channels were eliminated in the first step (removing $.70 \pm .99$ channels per participant on average), and the EEG data were re-referenced to an average reference. The PREP preparation

pipeline (Bigdely-Shamlo, Mullen, Kothe, Su, & Robbins, 2015) was then used, followed by the EEGLAB “clean rawdata()” pipeline. PREP uses a multitaper algorithm to remove line noise at 50 Hz and then adds a robust average reference after removing contamination by bad channels. The “clean rawdata()” procedure starts by detrending the EEG data with a .5 Hz FIR high-pass filter (order 1286, stop-band attenuation –80 dB, transition band .25 – .75 Hz). Channels that were flat-lined (below 5 μ V for a duration exceeding 5000 ms), noisy (based on the standard deviation within a channel), or outliers (correlation with other channels below .85 in more than 40 % of time points) were identified and removed (8.27 ± 3.97 channels per participant on average). Artifact Subspace Reconstruction was used to reconstruct epochs in the segmented data (see below) with abnormally strong power (>15 standard deviations relative to calibration data) [ASR; burst criterion: 15 (Mullen et al., 2013)]. Time windows that could not be reconstructed were removed. A lowpass filter of 40 Hz [pop_eegfiltnew() function in EEGLAB; sinc FIR filter; order: 86 (Widmann, Schröger, & Maess, 2015)] was applied. A subtraction method was used to remove EOG artifacts (Parra, Spence, Gerson, & Sajda, 2005). The Independent component analysis (ICA) automatically categorized and eliminated the muscle, heart, and remaining eye artifacts based Multiple Artifact Rejection Algorithm [MARA (Winkler, Haufe, & Tangermann, 2011, 2014)]. A spherical method was used to interpolate missing and eliminated channels.

By using the FieldTrip toolbox (Oostenveld, Fries, Maris, & Schoffelen, 2011), the neurophysiological data were segmented into intervals of 2s duration centered around the time of a response. In order to allow a comparison of neurophysiological data between Boundary and No-Boundary intervals, virtual response triggers had to be created for the No-Boundary category to have a locking point in both categories for subsequent analyses comparing these categories. Thus, a two-step segmentation procedure was applied: First, the neurophysiological data were binned into 2-s segments, which were categorized as either Boundary or No-Boundary intervals, depending on whether a response was given within those 2 s (i.e., according to the analysis of the behavioral data). If the distance between any two response markers was less than 4 s, the later marker was removed to avoid an overlap between segments. To mark respective time points in

No-Boundary intervals the following steps were taken: Since there were more No-Boundary than Boundary intervals, No-Boundary intervals were randomly selected with the number of No-Boundary intervals matching the number of Boundary intervals. This was done for each single participant. Then, again for each single participant, the Boundary intervals and the randomly selected No-Boundary intervals were sorted ascendingly according time in the video clip. This procedure also ensured the same signal-to-noise ratio in the data to be compared. Afterwards, time points of each real response marker in a Boundary interval were projected onto the selected corresponding No-Boundary intervals to generate virtual markers in these at the same position within the interval. In the second segmentation step, the neurophysiological data in the No-Boundary intervals were then locked onto the time point of the virtual marker, whereas in the Boundary intervals the intervals were locked to the response markers. A response-locked data analysis is the only possible strategy in this study, because there are (i) no temporally clearly distinct and separable stimuli as in more standard EEG paradigms and (ii) because the important aspect in event segmentation is the time point where an event boundary is set (which is indicated by the motor response/button press). Data from –1s to 1s relative to the respective marker (i.e., response marker or virtual marker) were included in the analyses. The segmentation procedure is schematically shown in Fig. 1.

2.4. Time-frequency analysis

In order to avoid edge effects in the time-frequency (TF) decomposition in the 2s intervals of interest (see 2.3), segments of 4s length (–2s–2s relative to the respective marker) were entered into the TF analysis. After TF decomposition, 1s of the data at the beginning and 1s of the data at the end of the 4s interval were discarded.

For each interval, TF analysis was conducted by applying Morlet wavelets for the frequency range from 3 to 30 Hz in frequency domain. The length of the used wavelets in standard deviations of the implicit Gaussian kernel was three. The number of cycles for the wavelet was linearly from 3 (3 Hz) to 12 (30 Hz). Then we calculated the average power for three frequency bands of interest at each time point: the theta frequency band (4–7 Hz), alpha frequency band (8–12 Hz), and

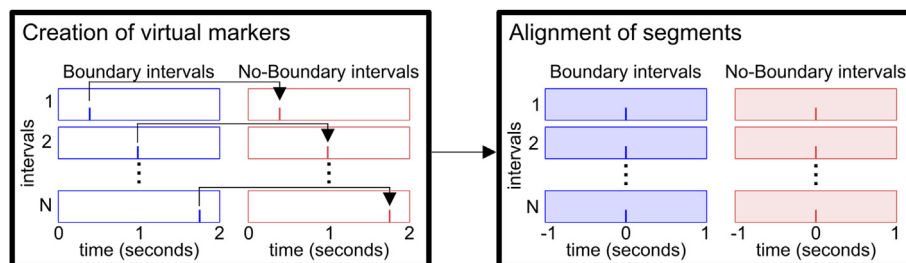


Fig. 1 – Schematic illustration of the segmentation of neurophysiological data.

Boundary intervals are displayed in blue; No-Boundary intervals are displayed in orange. The markers shown within the interval plots correspond to the response and virtual markers, respectively. First, No-Boundary intervals were randomly assigned to Boundary intervals. Virtual markers were placed in No-Boundary intervals at the same time point within the interval at which the button press occurred in Boundary intervals (left part). Subsequently, the segments were aligned based on the markers so that data from –1 to 1 sec relative to the marker position could be analyzed (right part).

beta frequency band (15–30 Hz). Next, in order to analyze the difference between Boundary interval and No-Boundary interval, a cluster-based permutation test as implemented in FieldTrip (Maris & Oostenveld, 2007) was computed for the time-frequency results of these three frequency bands. Of note, these comparisons were made using the averaged power of the frequency bands, since the hypotheses derived from the theory also refer to the averaged frequency bands. Samples were classified as members of a sample cluster if their *t*-value in the paired-samples *t*-test fell below $p = .050$. To define a cluster, at least two samples (e.g., two adjacent EEG channels or two successive time points) were required. The reference distribution of the permutation test was approximated by 1,000 random draws using the Monte Carlo method. A cluster was considered significant if the corresponding *p*-values fell below the critical alpha level of $p = .025$. Cohen's *d* was calculated using FieldTrip for each significant cluster (Meyer, Lamers, Kayhan, Hunnius, & Oostenveld, 2021).

2.5. Beamforming and source-level correlational analysis

A two-step beamforming analysis (Adelhöfer & Beste, 2020; Prochnow, Wendiggensen, Eggert, Münchau, & Beste, 2022) was performed to investigate the source activity of theta, alpha, and beta frequency bands. Further, the correlation of the difference of Boundary vs. No-Boundary interval between the theta, alpha, and beta band oscillations were calculated. In the following, the two steps of beamforming are described: The first step was Dynamic Imaging of Coherent Sources (DICS) beamforming (Gross et al., 2001), which employs a spatial filter to localize coherent brain regions and relevant voxels linked with the activity in theta, alpha, and beta frequency bands for the difference of the Boundary vs. No-Boundary interval. In the second step, Linearly Constrained Minimum Variance (LCMV) beamforming was applied to reconstruct the time courses of the power in the sources revealed by the DICS beamformer results (Van Veen, Van Drongelen, Yuchtman, & Suzuki, 1997). For the computation of the DICS beamforming, common spatial filters for both Boundary and No-Boundary intervals were calculated from the cross-frequency spectra of a Fast Fourier Transformation (FFT) on the averaged theta (4–7 Hz), alpha (8–12 Hz), and beta (15–30 Hz) frequency bands. The DICS beamformer projected the activity localization into a source space onto an evenly spaced grid (.5 cm resolution) created using the FieldTrip toolbox's forward model template, which is based on the standard Montreal Neurological Institute (MNI) space. The activity in the theta, alpha, and beta frequency bands was extracted for both Boundary and No-Boundary intervals. The power values in each interval were normalized using a decibel conversion. Clusters of the largest differences in theta, alpha, and beta band activity between Boundary and No-Boundary intervals in the DICS-beamformed data were defined by applying the Density-Based Spatial Clustering of Applications with Noise (DBSCAN) algorithm (Ester, Kriegel, Sander, & Xu, 1996) in MATLAB (2020b). Using this algorithm, only voxels within functional neuroanatomical regions were used in the next analysis steps. The obtained clusters (except regions belonging to the cerebellum) were labeled using the

Automatic Anatomical Labeling (AAL) atlas (Tzourio-Mazoyer et al., 2002). Power differences in the labeled regions were then thresholded to the top (or bottom, depending on the direction of the DICS beamforming contrast) 3 % of the power difference distribution within labeled regions to limit the analyses to voxels with strongest power differences of theta, alpha, and beta frequency band power. To identify the neighboring voxels, DBSCAN was ran with an epsilon of once the edge length and a minimum cluster size of two voxels. The DBSCAN results were further restricted by manual inspection of size and/or the affiliated AAL atlas labels. The selected clusters served as regions of interest for the subsequent analyses. Subsequently, an LCMV beamformer was used to obtain the time course of activity in the theta, alpha, and beta frequency bands in the chosen clusters (Van Veen et al., 1997). Based on the covariance data of the averaged data in each interval, a spatial filter was generated for each cluster and then multiplied with the preprocessed data. Time-frequency analyses were computed using Morlet wavelets, using linearly-spaced variable cycle numbers from 3 (3 Hz) to 12 (30 Hz), which were averaged over the selected voxels in each cluster/region of interest. In a time window of 1s before and 1s after responses (i.e., key presses) or virtual markers, correlations were calculated between differences in source activity reconstructed by LCMV beamforming in clusters in the theta, alpha, and beta frequency bands. A correlation matrix was created by calculating a Pearson's correlation across subjects for the source activity values at each time point (Adelhöfer & Beste, 2020; Prochnow, Wendiggensen, et al., 2022; Wendiggensen, Adelhöfer, et al., 2022). A false discovery rate (FDR) correction following the Benjamini-Hochberg method (Benjamini & Hochberg, 1995) was applied for each correlation matrix, to account for the potential rise in false positive results that is increased by the number of correlations. FDR correction of *p*-values results in *q*-values, which were only regarded as significant if $q < .050$. To ensure that the results were not due to type I error alone, the results of the correlation analyses were also evaluated using an alpha level corrected for the number of conducted correlational analyses (21 correlational analyses, see Results for details), resulting in a significance level of $q = .0023$.

2.6. Readiness potential

Since Boundary and No-Boundary intervals also differed with respect to the presence of a motor response, the time period of (pre-)motor processes should be determined since differences between Boundary and No-Boundary intervals in the frequency bands cannot be interpreted as an event segmentation-related process unbiased of motor activity in this period. To identify the time period of (pre-)motor processes, the activity before the response at electrode Cz was quantified, i.e., a readiness potential (RP) (Schurger, Hu, 'Ben' Pak, & Roskies, 2021; Travers, Friedemann, & Haggard, 2021; Travers & Haggard, 2021), based on the topographic distribution of the difference between Boundary and No-Boundary intervals in the time domain. This analysis indicates which time ranges (i.e., those in which no RP is evident) are interpretable in terms of event segmentation without a bias related to motor activity. Averaged voltage amplitudes were both

calculated for Boundary and No-Boundary intervals, as well as difference between them.

2.7. Statistics

To statistically analyze the behavioral data, mixed-effects logistic regression (R version 4.2.1, 'glmer' function) was performed to determine the effect of situational changes on the segmentation pattern. As in a previous study (Zacks et al., 2009), we built two mixed-effects regressions for different purposes: (i) predicting segmentation probability from the number of changes, and (ii) evaluating the relationship between each type of change and segmentation pattern. For both models, the random intercept for subjects was estimated to account for the variability between subjects, and odds ratios were calculated based on the coefficient results of fixed effect to be able to compare the influence of the different predictors. For (i), the number of changes irrespective of the type of change was counted for each 2s interval and fed into the regression analysis as predictor variable. Thus, the independent variable was the total number of situational changes (0–5), and the outcome was either a response by the participant indicating an event boundary within that interval or no response during that interval (i.e., Boundary vs. No-Boundary). For (ii), the predictor variables were the presence or absence (1 or 0) of situational change of each of the 9 situational change types within a 2s interval, and the outcome variable was the same as in (i). The variance inflation factor (VIF, R version 4.2.1, 'vif' function) was calculated to check for multicollinearity between the predictors.

In all neurophysiological analyses, the difference between Boundary and No-Boundary intervals was computed by subtracting the power values in No-Boundary intervals from power values in Boundary intervals. Thus, positive differences imply higher values in Boundary intervals than in No-

Boundary intervals, while negative differences suggest higher values in No-Boundary intervals than in Boundary intervals.

3. Results

3.1. Behavioral results

Regarding the number of situational changes in the 2s intervals, there were 518 intervals with no changes, 278 intervals with one change, 106 intervals with two changes, 52 intervals with three changes, 29 intervals with four changes and 4 intervals with five changes. The mixed-effects logistic regression model estimating segmentation probability as a function of the number of changes was converged with significant intercept (-2.375 , $z(28) = -16.30$, $p < .001$) and coefficient ($.429$, $z(28) = 29.96$, $p < .001$; OR = 1.536, 95 % CI = 1.493–1.580) for predictor in fixed effects. As shown in Fig. 2A, the probability of segmentation increased with increasing numbers of situational change.

The second mixed-effects logistic regression examining relations between each type of situational change and event segmentation was conducted for the 9 types of situational change. The amount of multicollinearity was calculated by using variance inflation factor (VIF), which was below 5 for each independent variable (Character = 1.500, Character-character = 1.386, Character-object = 1.023, Temporal = 1.298, Large space = 2.634, Small space = 1.213, Cause = 1.191, Goal = 1.443, Scene = 2.556), indicating that there was no multicollinearity issue in this model. This model was converged and odds ratios (OR) for coefficients in fixed effects are shown in Fig. 2B. Character (OR = 1.938, 95 % CI = 1.770–2.122), Character-character (OR = 2.195, 95 % CI = 1.958–2.460), Character-object (OR = 1.298, 95 % CI = 1.133–1.487), Temporal (OR = 1.581,

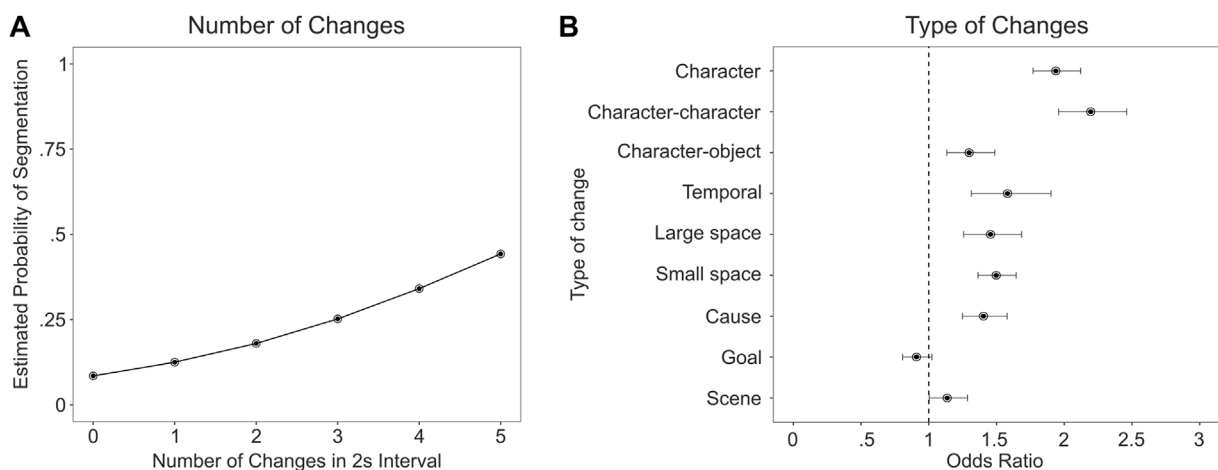


Fig. 2 – Behavioral results.

(A) Logistic regression results with the number of situational changes per interval as predictor (x-axis) and the probability of a response (i.e., segmentation) within an interval as outcome (y-axis). As the number of situational changes during the movie increased, viewers' probability of segmentation increased. (B) Odds ratios of the different situational changes from the logistic regression with the types of change within an interval as predictor (y-axis) and the probability of a response (i.e., a segmentation) within an interval as outcome (x-axis). Dots denote the mean odds ratio across participants, error bars show the 95 % confidence interval. The dashed line represents the reference for an OR of 1.

95 % CI = 1.314–1.902), Large space (OR = 1.456, 95 % CI = 1.257–1.685), Small space (OR = 1.498, 95 % CI = 1.363–1.645), Cause (OR = 1.403, 95 % CI = 1.248–1.578) and Scene (OR = 1.136, 95 % CI = 1.004–1.285) changes could significantly predict the pattern of segmentation. However, the remaining situational change type Goal (OR = .909, 95 % CI = .807–1.023) could not predict the segmentation pattern.

3.2. Oscillatory activity results on sensor and source level

Cluster-based permutation testing revealed significant differences of the time-frequency results in TBA, ABA, and BBA between Boundary intervals and No-Boundary intervals at the sensor level. Differences were calculated by subtracting No-Boundary intervals from Boundary intervals. Regarding TBA (4–7 Hz), as shown in Fig. 3A, cluster-based permutation testing revealed a positive cluster ($p = .024$; Cohen's $d_{\text{mean}} = .746$, Cohen's $d_{\text{min}} = .400$, Cohen's $d_{\text{max}} = 1.654$) at fronto-central electrodes from $-.71$ s to $.25$ s relative to a button press (i.e., perceived event boundary). The positive cluster indicates that TBA was stronger in Boundary intervals than in No-Boundary intervals. Further, a negative cluster ($p < .001$; Cohen's $d_{\text{mean}} = -.844$, Cohen's $d_{\text{min}} = -.665$, Cohen's $d_{\text{max}} = -1.032$) was also obtained for TBA at occipital, temporal and parietal electrodes from 0.2 s to 1 s relative to button press. The negative cluster indicates that TBA was stronger in No-Boundary intervals than in Boundary intervals. Concerning ABA (8–12 Hz), at the sensor level the cluster-based permutation test showed that there was higher activity in No-Boundary intervals than in Boundary intervals ($p < .001$; Cohen's $d_{\text{mean}} = -.853$, Cohen's $d_{\text{min}} = -.828$, Cohen's $d_{\text{max}} = -1.072$; Fig. 3A). The significant time window ranged from $-.77$ s to 1 s relative to button press at frontal, parietal, temporal and occipital electrodes. Regarding BBA (15–30 Hz), cluster-based permutation test also revealed significantly higher activity in No-Boundary intervals compared to Boundary intervals ($p < .001$; Cohen's $d_{\text{mean}} = -.801$, Cohen's $d_{\text{min}} = -.739$, Cohen's $d_{\text{max}} = -1.021$; Fig. 3A). These significant differences were found in the time window from -1 s to 0.5 s relative to button press and were found at frontal, parietal, temporal and occipital electrodes.

After establishing sensor-level differences between Boundary and No-Boundary intervals in TBA, ABA, and BBA, the sources of these differences were reconstructed using DICS beamforming (Gross et al., 2001) and were clustered using the DBSCAN algorithm (Ester et al., 1996) (for details, please see the Methods section). The DBSCAN algorithm revealed a positive cluster of TBA-related activity differences (Boundary > No-Boundary) in mid-frontal regions, encompassing the left and right supplementary motor areas (BA6), the left and right middle cingulum (BA24), the left superior/middle frontal gyri (BA8/BA9) and the left precentral gyrus (BA4, Fig. 3B). Further, there was a negative cluster of TBA-related activity differences (Boundary < No-Boundary) in right-hemispheric occipital regions, including right superior and middle occipital areas (BA18/BA19). Regarding the ABA at the source level, as shown in Fig. 3B, the DBSCAN algorithm revealed three negative clusters (Boundary < No-Boundary). One cluster each was located in the right hemispheric and left

hemispheric superior/middle frontal gyri (BA8/BA9), precentral gyrus (BA4), postcentral (BA1/BA2/BA3) and supra-marginal gyrus (BA40). The third cluster was located in the left inferior parietal cortex (BA40) and the left angular gyrus (BA39). Concerning the BBA at the source level, the beamforming analysis (Fig. 3B) revealed two negative clusters (Boundary < No-Boundary). One of them was located in the left supplementary motor area (BA6), the left middle cingulate gyrus (BA24), the left superior/middle frontal gyri (BA8/BA9), the left precentral gyrus (BA4) and the left postcentral gyrus (BA1/BA2/BA3). The other one was located in the right superior/middle frontal gyri (BA8/BA9) and the right precentral gyrus (BA4).

3.3. Readiness potential

Although BBA is often considered a reflection of motor processes, this cannot act as an explanation of the data in the current study: First, participants were instructed to press with their right hand, which should have induced contralateral left-hemispheric activity differences but in the present data we see bilateral BBA differences. Second, significant BBA differences are present after the response time point, which also argues against a pure association of BBA with motor processes in the current study. However, to further rule out that the effects obtained at the level of TBA, ABA and BBA are trivial motor effects that are only present in one condition, the readiness potential (RP) as a standard parameter of (pre-)motor activation processes was quantified (Schurger et al., 2021; Travers et al., 2021; Travers & Haggard, 2021). Regarding the readiness potential (RP), according to cluster-based permutation testing, there was a significant difference ($p = .003$) for voltage amplitude between Boundary and No-Boundary intervals from $-.133$ s to 0.070 s, i.e., there were RPs in Boundary intervals but not in No-Boundary intervals (Fig. 4).

The RP is only present in approx. 135 ms immediately before the response, so that only this period is probably confounded with motor processes. The rest of the 2-s interval around the key press and can therefore be interpreted in terms of event segmentation unbiased of motor activity. Since the effects obtained for ABA, TBA and BBA (see above) are not due to the time interval immediately before the boundary set (i.e., the motor response), the processes reflected by ABA, TBA and BBA are very unlikely to reflect mere motor processes unrelated to the actual cognitive event segmentation process.

3.4. Functional connectivity between frequency bands

To examine the inter-relation of theta, alpha and beta band dynamics, first, an LCMV beamforming procedure (Van Veen et al., 1997) was conducted in order to reconstruct the time course of the power of the respective frequency band in the established clusters. Regarding TBA, around the time of button press, i.e., around the time point of the perceived event boundary, there was increased power in Boundary intervals compared to No-Boundary intervals for the frontal source (ca. 0–200 ms; Fig. 5A) and decreased power in Boundary intervals compared to No-Boundary intervals in the occipital cluster (ca. 100–300 ms; Fig. 5A). Concerning ABA and BBA (Fig. 5A), there was decreased power (ca. -500 to 1000 ms for ABA; ca.

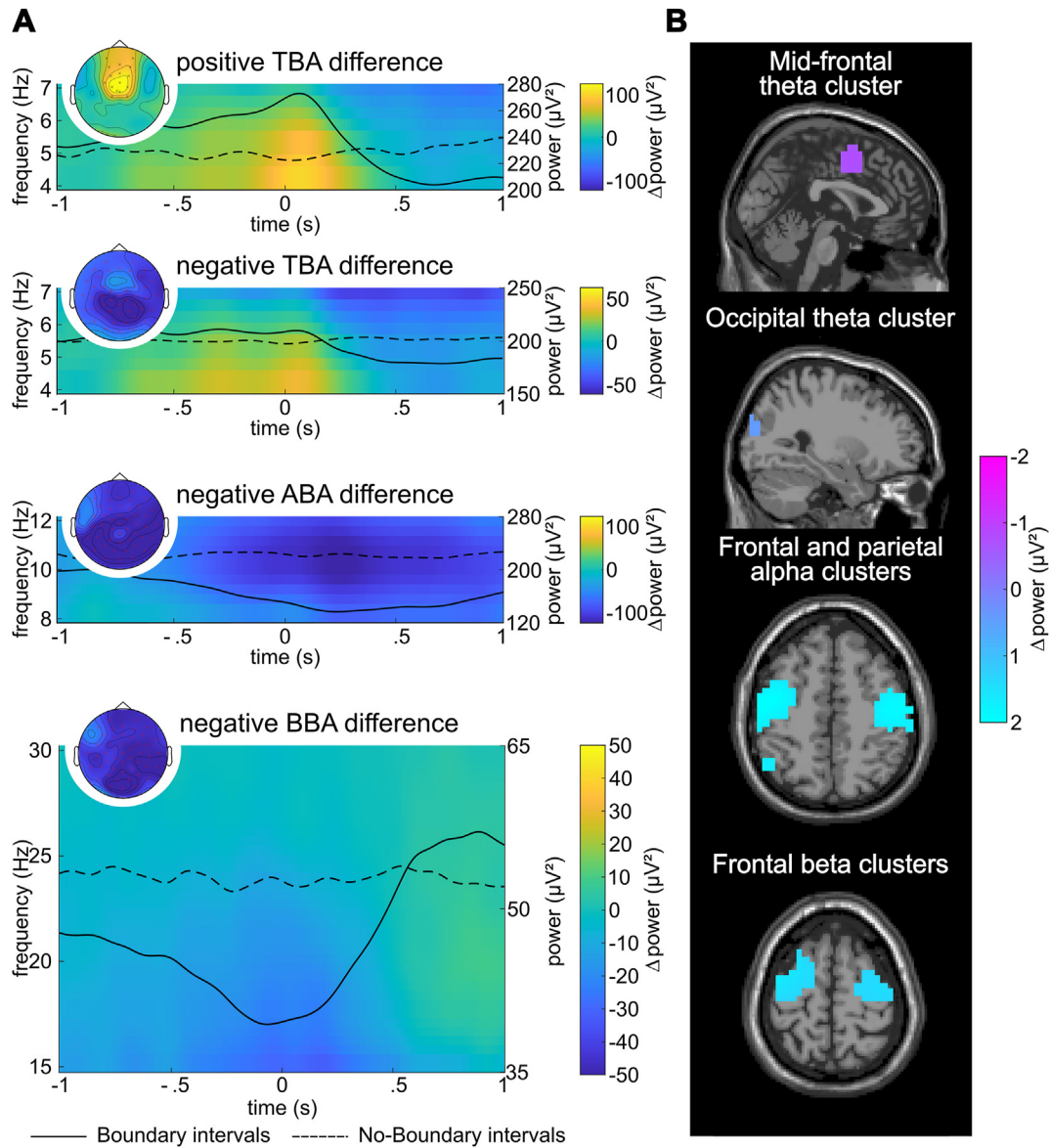


Fig. 3 – Time-frequency results in the intervals and their source localization in the brain.

(A) Results of the time-frequency (TF) analyses (TF plots) and the cluster-based permutation testing (topographic plots; differing from the calculations in the results section, the cluster-based permutation test on which these plots are based was calculated across the averaged time for display reasons). TF plots show the average of the power difference of the respective frequency band between Boundary and No-Boundary intervals over the significant electrodes in the cluster-based permutation testing (left x-axis indicates frequency). The overlaying lines depict the power time course of the averaged frequency band in the Boundary intervals (solid line) and the No-Boundary intervals (dotted line; right x-axis indicates power). (B) Results of the DBSCAN algorithm (top 3 %) after DICS beamforming. The scaling indicates the power difference. For all analyses, the values from No-Boundary intervals were subtracted from the values in Boundary intervals.

–100 to 400 ms for BBA) in Boundary intervals compared to No-Boundary intervals for all clusters. Finally, we examined possible inter-relations of TBA, ABA, and BBA by correlating the time courses of the power difference between Boundary and No-Boundary intervals at the source level (Dippel, Mückschel, Ziemssen, & Beste, 2017). To this end, 21 correlational analyses were conducted between the seven clusters established by the DBSCAN algorithm (after excluding double and self-correlations from the possible 7x7 correlations), and the results were corrected for the number of tests. Two

correlations had significant results ($q < .05$, FDR corrected): There was a negative cross-band correlation between the ABA source in left inferior parietal areas and the BBA source in left frontal areas ($r_{\min} = -.79$; $r_{\max} = -.55$, $q_{\min} < .001$, Fig. 5B). Further, there was a positive within-band correlation between the ABA sources located in the left and right frontal regions ($r_{\min} = .61$; $r_{\max} = .80$, $q_{\min} < .001$, Fig. 5B). Using an alpha-level corrected for the number of correlational analyses (21 correlational analyses, $q = .0023$) did not change the pattern of results (Fig. 5B) thus indicating the robustness of the finding.

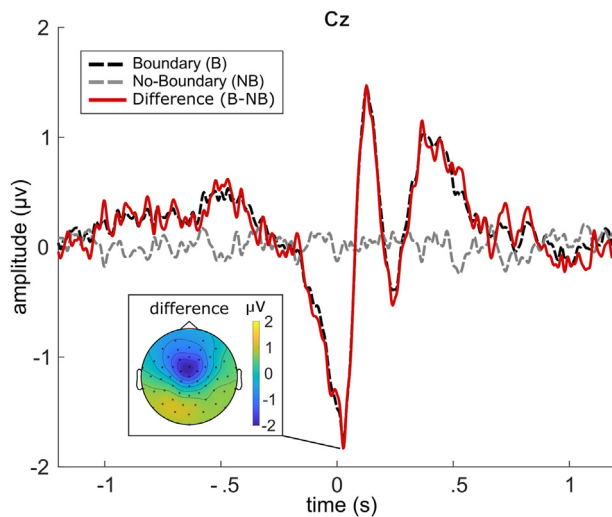


Fig. 4 – Readiness potential (RP) at channel Cz. RP waveform is shown by a negative difference of voltage (μV) amplitude between Boundary and No-Boundary intervals before responses (0s). With a 20 ms time window around the negative peak, the topographic map displays differences for all channels, showing typical characteristic of RPs that are observed in central and fronto-central regions.

However, out of the correlations obtained, only one of these revealed significant correlations around the time point of a response/virtual marker (cf. Fig. 5). In particular there was a negative correlation between ABA in parietal structures and BBA in frontal structures. The pattern of the correlations shows that ABA at the beginning of the analyzed time intervals (i.e., the first 500 ms) was inversely correlated with BBA for more than 500 ms after button press with which participants indicated the response of an event segment. As mentioned above, effects in TBA were also centered around the button press especially in frontal areas. Moreover, frontal areas associated with TBA modulations partly overlapped with areas involved in BBA modulations. Therefore, we examined whether the dynamics observed between parietal ABA and frontal BBA is related to the dynamics observed for frontal TBA. To obtain ABA-BBA correlation coefficient estimates for individual participant, a jackknifing procedure was applied similarly to previous research in order to avoid a bias in the data analysis (Adelhöfer & Beste, 2020; Prochnow, Wendiggen, et al., 2022). In this procedure, individual estimates of the ABA-BBA correlation coefficients (i.e., correlation coefficients at the single-participant level) were calculated by calculating correlation coefficients across participants by successively removing every participant from the data once. For each participant, the average over the correlation matrix of the two time courses was computed (Prochnow, Wendiggen, et al., 2022). This procedure results in a correlation coefficient estimate for each participant. To correlate the single-participant ABA-BBA correlation coefficients with the frontal TBA, the single-participant ABA-BBA correlation coefficients were Fisher-Z-transformed. The results of the correlation analysis are shown in Fig. 5C. There was a positive

correlation ($r_{\min} = .37$; $r_{\max} = .50$; $p_{\min} < .010$) between the strength of the fronto-parietal ABA-BBA connectivity and frontal TBA. For this correlation a temporal patterning was observed. Correlations were evident right after an event boundary was set and lasted for ~400 ms after the event boundary (i.e., the newly opened event segment).

4. Discussion

The current study examined how the human brain organizes the continuous stream of information about “what is happening now” into discrete segments with a focus on the temporal aspect of the underlying neural processes and thus on neural oscillatory activity. The behavioral data replicated previous work in showing the probability of segmentation increased as the number of situational changes increased (Zacks et al., 2009). The odds ratios indicated that for each type of situational change, changes in characters, character interactions and time were most predictive to mark a segment in the movie. The finding that there was a significant relationship between the number of changes and segmentation probability, and that previous findings were replicated (Zacks et al., 2009) rule out that participants performed random key-presses.

According to EST, important components of the event segmentation process are the working event model, which refers to the currently active representation of the situation, and the event schema, which refers to the long-term representation of how similar situations or events normally proceed (Zacks et al., 2007; Zacks & Sargent, 2010). Although there is some agreement in the estimation of event boundaries between observers, it is particularly important, especially in a measurement method with such a high temporal resolution as EEG, to account for inter-individual variability and thus to consider the individual responses of each subject (Niv, 2021; Sasmita & Swallow, 2022). For this reason, the information provided by the observers, i.e., the time of the key press, has been used as an indicator of an event boundary. The data analysis (cf. section on the relevance of motor processes) also revealed that there is no biasing effect of motor activity and the processes can be interpreted in terms of event segmentation unbiased of motor activity. Moreover, it is unlikely that the observed differences are due to differences in decision-making, as there is a constant decision process throughout the conducted task as to whether an event boundary is present or not.

Following EST, a segment boundary is set when a working event model, provided by information from the environment and long-lasting memory representations (i.e., event schemata) is no longer valid because the incoming information is too different from the working event model's expectations. Alpha band activity (ABA) has been shown to reflect the inhibitory gating mechanisms controlling access of information to a long-term “knowledge system” and working memory (Klimesch, 2011, 2012; Klimesch et al., 2007; Roux & Uhlhaas, 2014). Especially the access to episodic memories is controlled by ABA (Hanslmayr, Staresina, & Bowman, 2016) and such episodic memories show conceptual similarities to event schemata (Kurby & Zacks, 2008; Sargent et al., 2013; Zacks et al., 2009).

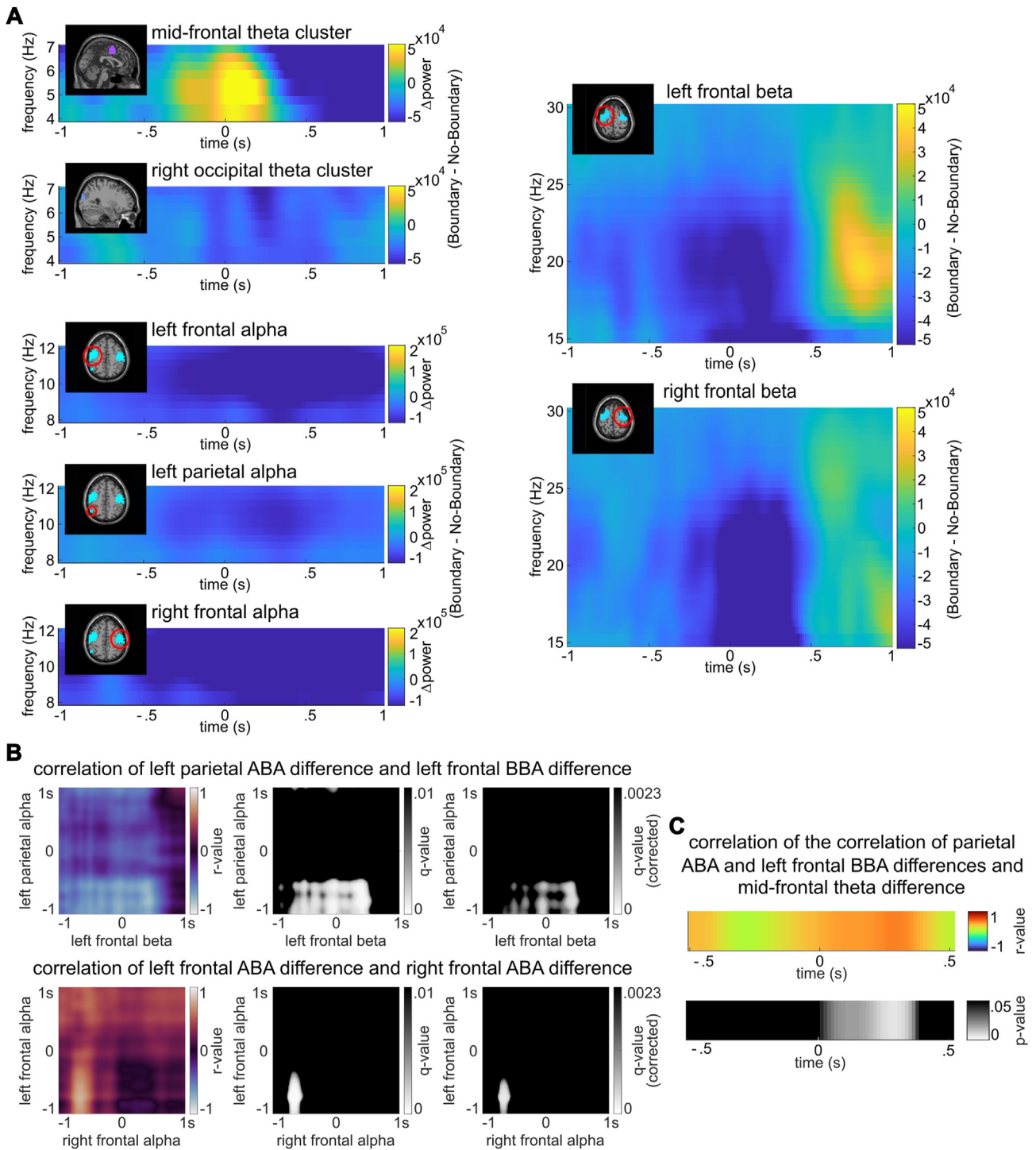


Fig. 5 – Power time courses and their correlations on the source level.

(A) Results of the LCMV beamforming. The plots show the power differences of Boundary minus No-Boundary intervals in the theta, alpha, and beta frequency bands in the clusters obtained by the DBSCAN algorithm. Time point zero denotes the time point of the response or the virtual marker, respectively. (B) Upper panel: Results of the correlation analysis between the power difference time courses in the parietal cluster in the alpha frequency band (y-axis) and the left superior frontal cluster in the beta frequency band (x-axis). Lower panel: Results of the correlation analysis between the power difference time courses in the left-hemispheric (y-axis) and the right-hemispheric (x-axis) frontal clusters in the alpha frequency band. In both panels, the left plot displays the r-values, the center plot displays the q-values with an alpha level of .01, and the right plot displays the q-value with the corrected alpha level of .0023, (C) Results of the correlation analysis between the Fisher-Z-transformed coefficients of the correlation between the parietal alpha and the left superior frontal beta frequency band (y-axis) and the power difference time courses in the fronto-central cluster in the theta-frequency band (x-axis). In all figure parts regarding correlation analyses, time point zero denotes the time point of the response or the virtual marker, respectively.

Thus, the modulations observed in ABA likely reflect the regulation of the access to the “event schema storage”. Increased ABA might indicate a more restrictive access to the episodic memories (Hanslmayr et al., 2016) and event schemata stored in it. The lower ABA in fronto-parietal structures was evident when a boundary was set by the participants. At this point the working event model needs updating (Zacks & Sargent, 2010), which implies a reduction of ABA-linked inhibitory gating. Corroborating this interpretation, these processes were associated with inferior parietal structures, known to be involved in the updating of task sets by incoming sensory information (Geng & Vossel, 2013). Furthermore, ABA in these areas was shown to reflect a gating of memory content retrieval (Prochnow, Eggert, Münchau, Mückschel, & Beste, 2022; Riddle, Scimeca, Cellier, Dhanani, & D’Esposito, 2020). Importantly, the correlational analysis of ABA modulations in parietal structures and beta band activity (BBA) modulations in superior frontal structures suggest that parietal ABA is a central mechanistic element in how the brain partitions the continuous stream of information into discrete segments.

The localization of BBA probably reflecting the maintenance and updating of working event models in prefrontal cortical areas is commensurable with the EST and its probable functional neuroanatomical implementation (Zacks & Sargent, 2010). A stronger modulation of parietal ABA was related to a smaller modulation of superior frontal BBA. Crucially, this correlation revealed a temporal pattern according to which ABA modulation at the beginning of the analyzed time intervals (i.e., the first 500 ms) was inversely correlated with BBA modulation for more than 500 ms after button press (indicating a segment boundary). BBA was also stronger when no segment boundary was set by the participants. BBA is thought to reflect the maintenance of the “status quo” and is stronger when the maintenance of the status quo is predicted (Engel & Fries, 2010; Jenkinson & Brown, 2011; Spitzer & Haegens, 2017). Since the current model of the ongoing situation needs to be maintained when no segment boundary is set, the increased BBA in time periods without a perceived event boundary corroborates the interpretation of BBA reflecting the maintenance of the working event model. However, increased BBA may also reflect an endogenously controlled transfer of latent memory content into current working memory (Spitzer & Haegens, 2017). From that perspective the correlational results imply that whenever parietal ABA-linked gating processes are strongly modulated, it is less necessary to adapt status quo monitoring or the transfer of latent memory content into working memory. The temporal patterning of the correlation between parietal ABA modulation and frontal BBA modulation indicates that parietal ABA-linked gating processes of incoming information affect frontal BBA-linked status quo monitoring. Taken together, the inter-relation between parietal ABA and frontal BBA reflects a mechanistic element in how the brain organizes and partitions the continuous stream of information into discrete segments. This is further corroborated by the findings in theta band activity (TBA).

Regarding TBA, there were activity modulations in middle and superior frontal regions overlapping with regions reflecting BBA effects. TBA activity in these regions was stronger when a segment boundary was set by the

participants (i.e., button press). According to EST, an event segment boundary is set when predictions based on the current working event model fail (Zacks et al., 2007; Zacks & Sargent, 2010). TBA reflects prediction error signaling and the unexpectedness (surprise) of events (Cavanagh et al., 2010, 2012; Cavanagh & Frank, 2014). The observed superior and medial frontal cortex TBA modulations may thus reflect the neural signature of failures in the working event model's predictions about how a situation has been supposed to evolve necessitating the closure of the event segment and the opening of a new one. Crucially, right after the indication of an event boundary (i.e., at the beginning of the new event segment), there was a strong correlation between frontal TBA modulation and the interplay of parietal ABA and frontal BBA: The stronger the modulation of TBA, the smaller the ABA-BBA inter-relation in the first ~400 ms after the indicated event boundary. Processes necessary to set event boundaries thus might be directly linked to the dynamics of parietal ABA-linked gating processes of incoming information that affect frontal BBA-linked status quo monitoring at the beginning of a new segment. However, when an event boundary was set and stronger TBA was evident in superior and medial frontal cortex, there was also reduced TBA in occipital regions. TBA in sensory regions may reflect “attentional sampling” processes necessary to detect changes relevant to behavior (Kienitz et al., 2018; Landau & Fries, 2012; VanRullen & Dubois, 2011; VanRullen et al., 2007). Thus, whenever an event boundary was set, it seems that TBA-related attentional sampling processes in occipital regions are weaker. Considering the temporal pattern of modulations, this implies that when a new event segment is opened, the attentional focus is selectively put on specific, relevant information in the environment, presumably in order to be able to establish a new event model.

4.1. Limitations and future directions

Although it was ensured in the current study that the obtained effects on the neurophysiological level are not due to pure motor activity, it needs to be kept in mind that the time of the key press by the participant is only the motor reflection and thus an estimation of the time of the actual event boundary. However, as in all cognitive (neuroscience) studies, particularly if they are relying on such a subjective assessment by the participant as event segmentation studies, there is an inevitable delay between the cognitive process of interest and the response given by the participant (Niv, 2021). Thus, since the investigation of event segmentation heavily relies on the subjective assessment of the participant, asking the participants for their response is the only way to assess their assessment of event boundaries.

Future studies on the neurophysiological underpinnings of event segmentation might also take into account established frameworks regarding the operating principles of the brain, e.g., intrinsic neural time scales (INT) and the related concepts of temporal receptive windows (TRW) and integration and segregation (Golesorkhi et al., 2021; Hasson, Yang, Vallines, Heeger, & Rubin, 2008; Lerner, Honey, Silbert, & Hasson, 2011; Wolff et al., 2022). Both the EST and the INT approach assume a hierarchical processing of information and consider prediction errors to be important for segregating/partitioning

different perceived elements (Golesorkhi et al., 2021; Hasson et al., 2008; Lerner et al., 2011; Wolff et al., 2022). However, while the EST is a cognitive theory the elements of which have been related to activity in different brain regions, the INT approach considers rather basic neurophysiological processes. Thus, future studies might aim to find a connection of both concepts in order to link cognitive and neuroscientific theories.

5. Conclusions

In summary, the study reveals a mechanistic chain of processes at the level of oscillatory activity during the segmentation of the continuous stream of information into meaningful segments. The close interconnection of event schemata from long-term memory and the working event model is represented by an interplay between ABA and BBA in frontal and parietal areas. This interplay is in turn related to frontal TBA modulations, which likely reflect the detection of prediction errors of the current working event model, revealing the highly significant role of matching prediction and environmental information for event segmentation. This study thus integrates neurophysiology and cognitive theory to better understand how the human brain operates in rather variable and unpredictable situations. Therefore, it represents an important step towards the study of neurophysiological dynamics in ecologically valid and naturalistic settings, aiming to fill a critical gap in our knowledge of the temporal dynamics of how the brain structures natural scenes.

Author contributions

AP: Conceptualization, Methodology, Investigation, Writing – Original Draft, Visualization, Supervision. XZ: Methodology, Software, Formal analysis, Investigation, Writing – Original Draft, Visualization. FG: Investigation, Writing – Original Draft, Visualization. PW: Methodology, Formal analysis, Writing – Review & Editing. VR: Conceptualization, Resources, Writing – Review & Editing, Funding acquisition. BH: Conceptualization, Writing – Review & Editing, Funding acquisition. CB: Conceptualization, Methodology, Resources, Writing – Original Draft, Supervision, Project administration, Funding acquisition. All of the authors reviewed and approved the manuscript for publication.

Code and data availability

The collected data and the code written by the authors and used for the data analysis is deposited under the following link: <https://osf.io/zsfx8/>

Open practices

The study in this article earned Open Data and Open Materials badge for transparent practices. The data and materials used in this study are available at: <https://osf.io/zsfx8/>

Declaration of competing interest

The authors declare no conflict of interest.

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