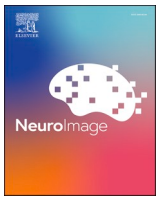
NeuroImage 317 (2025) 121335

Contents lists available at ScienceDirect

NeuroImage

journal homepage: www.elsevier.com/locate/ynimg



Brain signatures of predictive and reactive strategies in a simple delayed reaction time task: an EEG study

Arianna Brancaccio *, Marco Tagliaferri, Carlo Miniussi, Luigi Cattaneo

Center for Mind/Brain Sciences - CIMeC, University of Trento, Rovereto, TN, Italy

ARTICLE INFO

Keywords:
Internally-driven
Externally-driven
Sensorimotor task
EEG
ERPs
Time-frequency

ABSTRACT

In a simple pre-cued sensorimotor task, two behavioral patterns emerge spontaneously on a trial-by-trial basis, characterized by a bimodal distribution. The early and the late patterns are likely the product of two distinct mutually exclusive strategies: predictive and reactive. Predictive behavior is driven by an internally generated, top-down mechanism, allowing participants to estimate the timing of the target stimulus. In contrast, reactive behavior relies on an externally-driven, bottom-up mechanism, where participants wait for the target stimulus before responding. In this exploratory study, we aimed to further validate the existence of these two strategies by showing they are distinguishable based on EEG patterns, analyzed in both temporal and frequency domains using different metrics, including event-related potentials (ERP), time-frequency representations, modulation index, inter-trial phase coherence, and connectivity. Early behavioral responses showed an augmented ERP, named contingent negative variation, in comparison to late behavioral responses. This validate the hypothesis of a top-down, predictive mechanism, based on temporal estimations. In addition, we showed that EEG dynamics differentiated the two conditions in the SET period. This result further corroborates the hypothesis that the commitment to one strategy does not occur before trial onset but rather builds up during the SET period. When analyzing the electrical activity after the GO-signal, we observed that early and late responses are associated with distinct EEG features, with early behavior displaying feature typical of top-down processes. In our experiment, the two behaviors occurred naturally, without external manipulations that could introduce confounding cognitive demands and obscure genuine differences in EEG patterns between strategy-dependent conditions.

1. Introduction

1.1. Predictive vs. reactive behavior in a simple detection task

Imagine being an athlete at the starting block, waiting for the start signal. Successful behavior depends on the capacity to stand still before the GO-signal, thus avoiding a false start, and to move as fast as possible after the start. Studies of human behavior have shown that, in a pre-cued simple reaction time (RT) task (such as the ready-set-go scenario of the starting block), achieving fast RTs benefits strongly from the regularity of the fore-period (or SET-period), as has been repeatedly shown empirically (see (Niemi and Näätänen, 1981; Schmidt, 1968) for a review of classical experimental psychology literature). Interestingly, anticipatory behavior has a distinctive signature, i.e., shortening of RTs well below the possibilities of bottom-up, reactive behavior. Whenever regularity is present and can be learned by the agent, responses will be way shorter than the RT to an external trigger whose onset can be predicted (Schmidt, 1968), and indeed, such responses should not be referred to as true "reaction" times at all, since they are entirely predictive in nature. The cut-off, in terms of response timing, between reactive and predictive strategy changes according to several factors, including sensory modality, age, and duration of the SET-period, to as low as 133 ms (as for example in (Adams and Chambers, 1962; Adams and Creamer, 1962)). Most experimental data on the distribution of the time of responses in conditions of uncertainty of the SET-period (i.e., not allowing any predictive strategy) show fastest responses between 160 and 200 ms, depending on the studied population. Going back to the initial "starting block" analogy, official sport regulations set to 100 ms the limit for genuine "reactive" responses to the auditory cue in sprint starts (Milloz et al., 2021). Interestingly, we recently showed in two separate manuscripts that, the well-known advantage in terms of response times of the regularity of the SET-period is correspondent to the appearance of "super-early" responses that are not part of a tail of the RT distribution, but rather represent an easily discernible separate

* Corresponding author.
E-mail address: arianna.brancaccio@unitn.it (A. Brancaccio).

https://doi.org/10.1016/j.neuroimage.2025.121335
Received 5 February 2025; Received in revised form 5 June 2025; Accepted 16 June 2025
Available online 17 June 2025

component in the distribution with a separate peak, that can be modelled as a distribution distinct from that of the conventional reactive behavior. (Cattaneoand Parmigiani, 2021; Tagliaferri et al., 2023). Rendering the SET-period unpredictable abolishes the early predictive component. (Tagliaferri et al., 2023). This bimodal distribution allows to clearly label individual responses as predictive or reactive. Interestingly, adoption of the reactive strategy occurs implicitly, without participants being aware that the SET period is predictable, and there are considerable variations in the individual propensity towards either strategy. In the population ($n = 20$) described in (Tagliaferri et al., 2023) the percentage of predictive trials ranged between 10 and 40 % of all trials. In the trade-off between speed and accuracy, predictive strategies are faster, but more prone to anticipation errors, while reactive strategies are slower, but more accurate. Summing up, when challenged in a sensorimotor task with emphasis on speed, the brain is capable of picking up regularities in the timing of the cues so that it can generate predictions on its occurrence (Van Der Steen and Keller, 2013). It is interesting to note that the two behavioral strategies are mutually incompatible. The predictive strategy consists in moving without actual available sensory information, estimating the time of onset of the GO-signal based on prior knowledge. Differently, the reactive strategy consists in waiting for the GO-signal, bottom-up processing its sensory characteristics, and mapping the sensory cue onto a movement commitment. The bi-modality of the distribution of RTs clearly indicates that the two behaviors are not at the two extremes of the same spectrum, but rather represent two different entities.

1.2. Neural bases of predictive vs. reactive behavior

Previous literature suggests that predictive and reactive behaviors engage distinct neural systems, reflecting a dynamic interplay between top-down and bottom-up mechanisms. Evidence from non-human primate studies indicates that reactive behavior, which relies on sensory-driven processes, is associated with activity in the ventral premotor cortex and inferior frontal gyrus (IFG) (Hoshi and Tanji, 2004; Rizzolatti et al., 2014). In contrast, predictive behavior, guided by internally generated timing, is thought to involve the supplementary motor area (SMA) and pre-SMA, which are key regions for temporal anticipation and motor planning (Mita et al., 2009; Shima and Tanji, 2000). Human studies complement these findings, highlighting that the superior frontal gyrus (SFG) and IFG are critical to strategy selection. A recent study from our group (Tagliaferri et al., 2023) demonstrated that single-pulse TMS applied to the SFG during the SET period (jittered between 400 and 800 ms) increased predictive behavior, while single-pulse TMS applied to the IFG in the same period increased reactive behavior. The stimulation was targeted to the left hemisphere as participants performed the task with their right hand. These results suggest that the SFG and IFG play distinct roles in guiding predictive and reactive behavior, respectively, and that these regions are connected by the frontal aslant tract (FAT), which mediates their competitive interaction. Notably, the study showed that strategy choice remains flexible during the SET period, with TMS applied between 400 and 800 ms in the preparatory phase still capable of biasing the strategy choice. Nevertheless, the precise temporal unfolding of strategy choice during the SET period remains unclear. Therefore, incorporating electroencephalography (EEG) could provide valuable insights by capturing the neural dynamics underlying the decision-making process.

1.3. Aim of the study

In the present work, we aim to study with high temporal resolution, i.e., by means of electroencephalography (EEG), the brain dynamics associated with spontaneous Predictive vs. Reactive behaviors. First, our objective is to corroborate the previous finding of two mutually exclusive strategies that arise in a “starting block” task where the target onset is predictable (like in Cattaneoand Parmigiani, 2021; Tagliaferri et al., 2023). Moreover, we further aim to show that the Predictive and Reactive behavior differ in terms of EEG patterns, as this is essential to move beyond the inference of the existence of the two strategies based solely on behavioral results. In fact, identifying distinct EEG patterns for each condition (Predictive and Reactive) would strengthen the hypothesis that two mutually exclusive strategies are available when the temporal prediction of a target is possible. Finally, as introduced above, previous research (Cattaneoand Parmigiani, 2021; Tagliaferri et al., 2023) has shown that applying spTMS to the SFG or IFG during the SET period biases participants towards the Predictive or Reactive strategy, respectively. This indicates that both strategies are available during the SET period, as their build up can be influenced by TMS. Therefore, our further aim is to examine whether EEG differences can reveal the temporal unfolding/time course of strategy choice. This would shed new light on which neurophysiological patterns, when targeted with TMS, influence the adoption of either strategy. To our knowledge, this is the first study to characterize internally- (Predictive) and externally-guided (Reactive) behaviors based solely on participants’ implicit choice, without external manipulations, thus enhancing the validity of comparative analysis. The study will compare and characterize the two types of behavior in terms of all EEG signal features, from the timing and amplitude of brain responses (i.e., event related potentials - ERP) to their oscillatory dynamics (i.e., time-frequency representations - TFR, modulation Index - MI, inter-trial phase coherence - ITPC, and connectivity). Given the lack of prior studies on oscillatory dynamics in this task, we adopted an exploratory approach for these analyses.

2. Methods

2.1. Participants

Participants were recruited from the general population through public advertisement. They were monetarily compensated for their participation. We included in the study healthy right-handed individuals aged 18–50 years with normal or corrected to normal vision. Exclusion criteria were the presence of neurological or psychiatric disorders. In total, twenty-three participants were recruited for this experiment. A further exclusion criterion, to be applied post-acquisition of the data was related to performance in the task: participants who showed <100 trials in any of the two conditions (Predictive or Reactive) were not considered for further analysis. Only one participant on 23 was excluded for this reason (showing only 5/250 trials categorized as Predictive). The resulting population on which planned analyses were performed was made of 22 participants (11 females, mean age 27 $\pm$ 3 years). All participants provided written informed consent to participate. This study was conducted in conformity with the Declaration of Helsinki and was approved by the local Ethics committee of the University of Trento (protocol 2020_035).

2.2. Task

In this study, we employed the same pre-cued simple RT task used by Cattaneoand Parmigiani (2021) and Tagliaferri et al. (2023), resembling a “ready-set-GO” scenario. *Fig. 1* shows a schematization of a single trial. Participants were seated on a comfortable chair in a dimly lit room and were instructed to position their head on a stationary chinrest throughout the duration of the experiment, maintaining a distance of 60 cm from a 27-inch standard monitor (refresh rate 60 Hz). A response keyboard was positioned in front of them. Stimulus presentation was conducted via MATLAB (v.2018b, Psychtoolbox) scripts. The experimental task employed in both experiments was a pre-cued GO-task, involving phases of "rest", "set-period", and "GO-signal + response". Refer to Fig. 1 for a visual depiction of the trial structure. Participants were alerted on the upcoming GO-signal by the set-period, which had a fixed duration of 900 ms. The phase of each trial was indicated to the participant by the color of a circle at the center of a white screen: gray

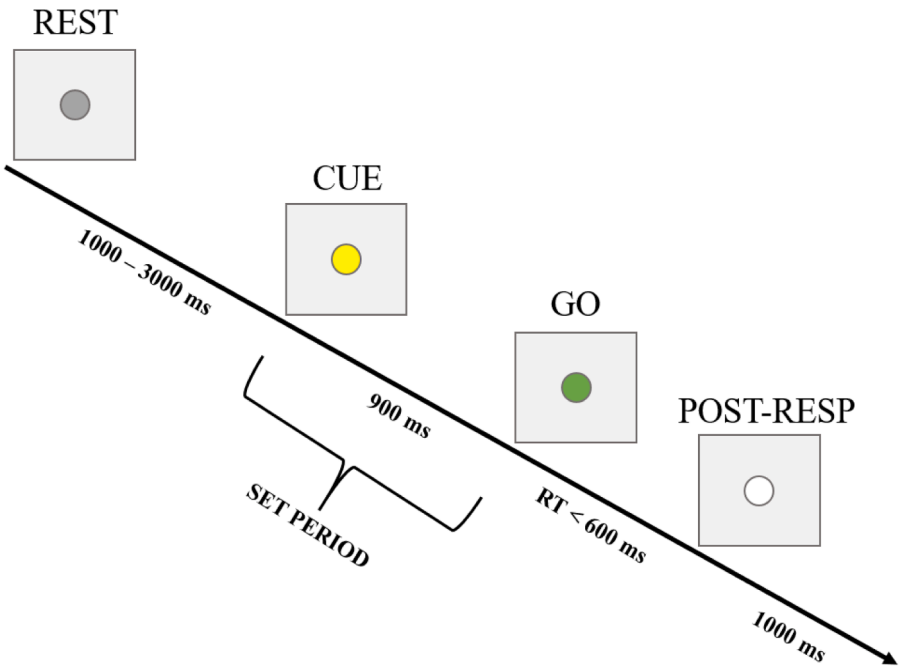


Fig. 1. Schematization of trial timeline.

for rest, yellow for the set-period, and green for the GO-signal. They were instructed to respond by pressing the spacebar with their right index finger as quickly as possible after seeing the GO signal. Participants received feedback if they responded before the GO-signal (false start), displayed as "too early" on the screen, or too late, indicated as "too late" if the response occurred after 600 ms from the GO-signal. The complete script for stimulus presentation can be found and downloaded at: https://osf.io/x76cm/. The duration of the gray circle (rest phase) varied randomly based on a square-wave function, ranging from 1000 to 3000 ms. The period from cue onset to GO signal onset (SET period) was fixed at 900 ms. The green circle period (from the presentation of the GO signal) was fixed at 600 ms. Before the actual experiment started, participants familiarized themselves with the task in a series of 15 trials. The actual experiment consisted of 7 - 9 blocks (depending on whether the participant was feeling too tired and wanted to stop the experiment) of 50 trials each. To demonstrate the learning process and participants' diligent engagement throughout the whole experiment, we include Suppl. Fig 1 which shows the ratio of predictive to reactive trials averaged across subjects over blocks.

2.3. EEG data acquisition

EEG signals were acquired from a standard 10–20 EEG layout cap (Easycap) connected to a g.HIamp amplifier (g.HIamp amplifier), with 64 electrodes (for the complete electrode list, refer to the Supplementary Material). Data were acquired using g.Recorder, software (g.tec version 5.16.00) with a sampling rate of 5000 Hz (DC). During recording the AFz and Oz electrodes were used as the ground and reference electrode, respectively. The skin–electrode impedance was kept below 8 kΩ. Trigger marks at the three events of interest (cue, GO, response) were sent to the EEG system using a customized MATLAB script (MathWorks®, Inc., Massachusetts, USA).

2.4. Data-driven definition of participant's strategy in single trials

In this work, we wanted to investigate how the EEG neural correlates would differ between the trials belonging to the two different conditions as determined by either the Predictive or the Reactive strategy. These two strategies differentiate mainly on the basis of the response time, with predictive responses being faster than reactive ones, arranged in to only partially overlapping distributions. Given this assumption, a clustering algorithm can be used for unsupervised classification of the two conditions. Therefore, to label single trials, we determined the split point between the two RTs' distributions using an unsupervised data-driven approach. For this, we used a k-means clustering algorithm assuming a priori 2 classes for the RTs of each participant. Responses given earlier than 100 ms before the GO signal and later than 600 ms after the GO signal were excluded from the classification because considered as outliers (Tagliaferri et al., 2023). Through this data driven procedure, trials belonging to the Predictive and Reactive conditions were defined and then used for the EEG analysis.

2.5. Data analysis

All the following analyses were implemented using functions available in the EEGLAB and Fieldtrip toolbox (Oostenveld et al., 2011) and custom MATLAB code.

2.5.1. EEG data preprocessing

Prior to epoching, the continuous raw EEG data were filtered between 1–90 Hz using a zero-phase, 4th-order high and low pass Butterworth filter. Additionally, a zero-phase, 4th-order Butterworth bandpass notch filter was applied between 48–52 Hz to reduce 50 Hz power line noise. This allowed for smooth frequency attenuation around the notch frequency band (no distortion for neighboring frequencies of interest, i.e., $\leq$47 Hz), preservation of signal phase and exclusion of edge effects in the times of interests. Furthermore, EEG data were downsampled from 5000 Hz to 1000 Hz. At this point, epoching was implemented by time-locking the signal to 1) the Cue (onset of the yellow circle) and 2) participants' Response, treating them as separate analyses. To explore activity time-locked to the Cue signal onset (yellow circle onset), epoching was implemented between −1500 to 2400 ms around the Cue, therefore including also the GO signal onset which is always at 900 ms from the Cue. Afterwards, bad channels were interpolated and epochs with muscular artifacts were discarded based on visual inspection of the data. After manual bad trials rejection, independent component analysis (ICA) based on the fastica algorithm (as implemented in EEGLAB) was performed. Thanks to this procedure,

components associated with blinks and saccades were discarded. Furthermore, to explore activity time-locked to participants' Response, a second locking was implemented this time between −2000 to 900 ms around response.

2.5.2. Event related potentials

In our trial we identified two main events of interest for ERP analysis, namely the Cue and the participants' response. We computed ERP using the activity time locked to both events, separately. In the first case, around the cue (−1500 to 2400 ms onset of the yellow circle), while data from −500 ms to 0 ms were used for baseline correction. In the second case, the epoch was defined from −2000 ms to 900 ms around the participant's response. In this case we chose the interval between −2000 ms to −1500 ms as a baseline, to avoid including in the baseline time points following the presentation of the cue. All the subsequent analyses are identical for both events of interest. For each subject, we computed grand-average ERPs for both the Predictive and Reactive conditions (see "Data-driven definition of experimental conditions" Section for details on trials type classification). Furthermore, we performed a statistical analysis in order to identify differences in ERPs between the two experimental conditions. We implemented a cluster based non-parametric paired-samples *t*-test (number of randomizations = 1000). This procedure identifies, in time and space (channels), clusters of significantly different activity between the two conditions, controlling also for the multiple comparison problem by clustering. We set the statistical thresholds to $\alpha = 0.01$ for both the first level and cluster statistics and the minimum number of neighborhood channels for clustering equal to 2. In the case of data time-locked to the cue onset, we limited the time of interest for computing the statistics between 0 and 900 ms around cue onset (i.e., the total duration of the yellow circle, until the appearance of the green GO signal). Instead, in the case of data time locked to the response, we limited the time of interest for computing the statistics between −500 to 500 ms around participants' response. These time windows were selected to investigate ERPs typically associated with anticipation and motor tasks, like the contingent negative variation (CNV) and the P300. The Bereitschaftspotential instead will not be examined in this context, as it is typically associated with voluntary movements, whereas this study focuses on pre-cued movements. (Hohnsbein et al., 1998; Ullsperger et al., 1988;).

2.5.3. Time-frequency representation

As for the ERPs analyses, in our experiment we considered two main events of interest, namely the Cue and the participants' Response. Separately for Predictive and Reactive conditions and for data time-locked to the Cue and to participants' Response, we computed time resolved Fourier spectral representations. For activity time-locked to the Cue onset, TFRs were computed between −1500 ms to 1500 ms around the cue onset. Instead, when the event of interest was the participants' Response, TFRs were computed between −2000 ms to 900 ms. In both cases, the time window length was frequency dependent and defined as 3 oscillation cycles and it was moved in steps of 5 ms. As regards the frequency domain, all the Fourier spectral amplitudes were computed in the range 4–70 Hz. For the Fourier analysis we used a multi-taper approach, based on Discrete Prolate Spherical Sequences, with a frequency dependent bandwidth, defined as 1/3 of the frequency of interest. Separately for the TFR time-locked to the Cue and participants' Response, we performed statistical analyses to identify time resolved spectral differences between the two experimental conditions (Predictive vs. Reactive). We implemented a cluster based non-parametric paired-samples *t*-test (number of randomizations = 1000). This procedure identifies, in time and space (channels), clusters of significantly different activity between the two conditions, controlling also for the multiple comparison problem by clustering. For cue onset time locked TFRs, we ran the cluster statistics twice with two different statistical thresholds, namely $\alpha = 0.01$ and $\alpha = 0.05$ for both the first level and cluster statistics. To ensure a comprehensive analysis, the TFR was tested at two different alpha levels (0.01 and 0.05) to balance sensitivity of the statistical test with respect to the effect size. This allowed us to detect robust effects (alpha = 0.01) while also exploiting weaker effects that cannot emerge considering a threshold of 99 % for null-hypothesis rejection. The minimum number of neighboring channels for clustering was equal to 2 in all analyses. Cluster analysis was computed to test for differences between Predictive and Reactive trials in the frequency bands of interest, namely θ (4–7 Hz), α (8–13 Hz), β (15–35 Hz) and low-γ (36–47 Hz). Although Fourier coefficients were computed up to 70 Hz, only frequencies up to 47 Hz were analyzed, as higher frequencies in EEG data are generally less reliable due to their susceptibility to noise and reduced signal quality. In the case of TFR spectra computed on data time-locked to the cue onset, we limited the time of interest for computing the statistics between −500 to 600 ms around the Cue. This was done in order to 1) test for potential differences in TFR spectra before cue presentation between Predictive and Reactive conditions and 2) avoid including in the analysis time points after 600 ms from cue onset, given that differences from this time point could be potentially confounded by the anticipated responses in Predictive compared to Reactive trials. Differently, for TFR spectra computed on data time-locked to the participants' Response, we limited the time of interest for computing cluster statistics between −500 to 500 ms around response.

3. Results

3.1. Data-driven definition of experimental conditions

Fig. 2A shows the superimposed individual Gaussian kernel density estimates of the 22 participants' RTs in blue, together with the average Gaussian kernel density estimate of the whole population in red. As it can be appreciated from this figure, the prediction of a bimodal distribution in the RTs was confirmed and is comparable to what Tagliaferri et al. (2023) also found. Crucially, as shown in Fig. 2B, the k-means clustering managed to separate two classes of RTs for each participant, with the mean Predictive distribution center being at 22 ms from GO onset and the mean Reactive distribution center being at 228 ms from GO onset. The mean separation point, which is the split point between predictive and reactive trials, was 101 ms (±19). Overall, the group average amount of predictive trials was 150 (±33) and the group average amount of reactive trials was 161 (±42). Suppl. Fig. 1 also confirms this trend, showing a progressive increase in predictive/reactive trial ratio across blocks. This trend underscores that participants adapted to the task over time, favoring predictive strategies without a notable decline in performance, even in later experimental blocks.

3.2. ERPs

The results obtained from the cluster statistical analysis revealed significant differences in ERPs between the Predictive and Reactive conditions both for data time-locked to cue onset and for data time-locked to participants' response. Regarding the results from the cluster analyses computed over data time-locked to the Cue, Fig. 3 shows the significant negative cluster emerged between 650 ms to 900 ms from cue onset (p-value < 0.0001).

As fo the results obtained from the cluster analyses computed over data time-locked to the participants' response, Fig. 4 shows the three significant clusters emerged from the comparison between ERPs evoked around the response in the Predictive vs. Reactive conditions. Clusters in Fig. 4 are presented in temporal order. Fig. 4A shows the first significant positive cluster emerging between - 340 ms to −180 ms with respect to participants' response (p-value <0.01). Fig. 4B shows the negative significant cluster emerging between −17 ms to 125 ms with respect to participants' response (p-value <0.0001). Fig. 4C shows the significant positive cluster emerging between 215 ms to 405 ms with respect to participants' response (p-value <0.0001).

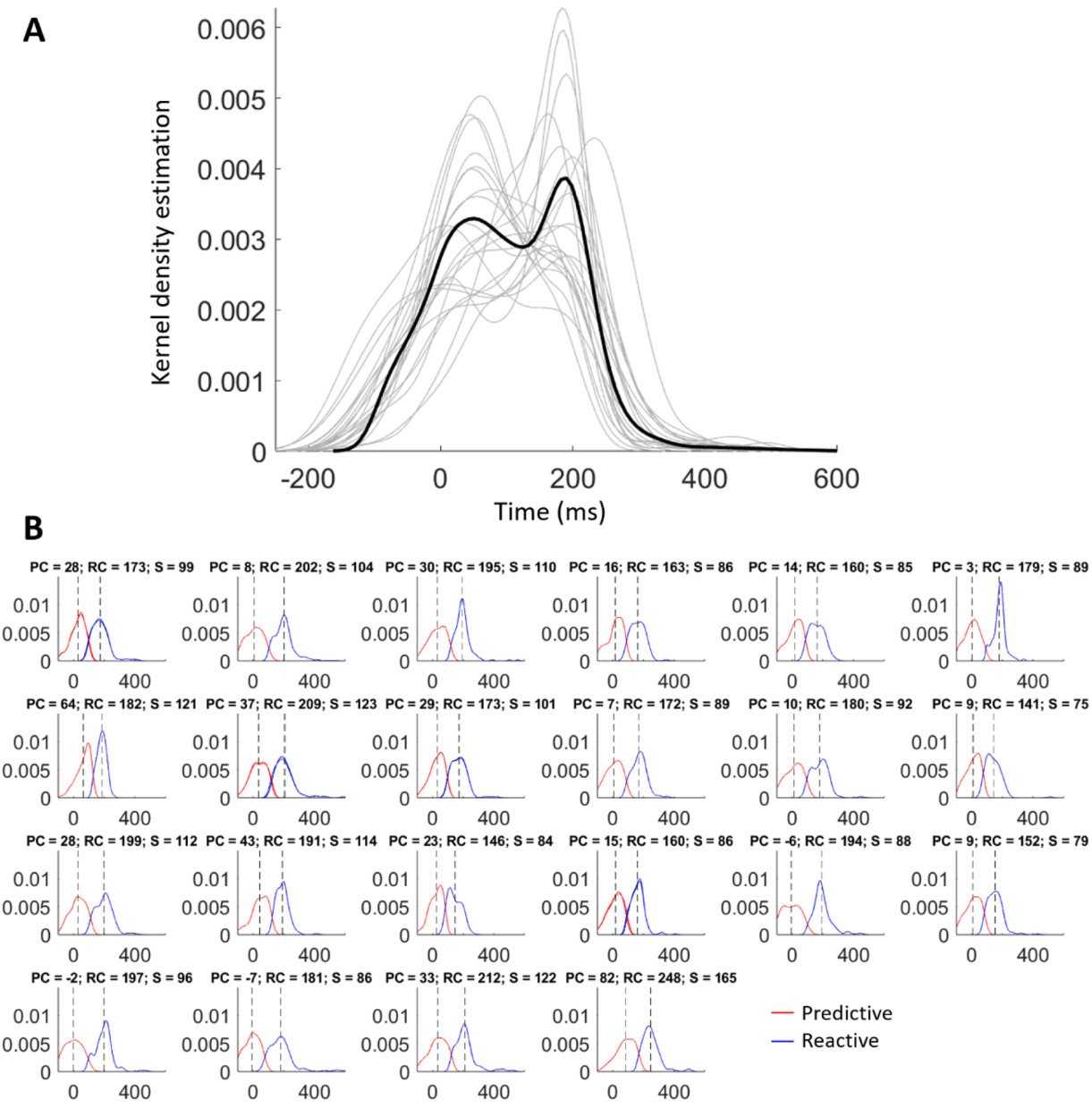


Fig. 2. A) Superimposed individual Gaussian kernel density estimates of the 22 participants (grey lines) and mean Gaussian kernel density estimate of the whole population (black line). 0 refers to the GO signal onset. B) Gaussian kernel density estimates for the two distributions found by applying k-means classification separately on each participant's RTs. Dotted lines indicate the modes for the two distributions. PC refers to the centre of the predictive RTs' distribution. RC refers to the centre of the reactive RTs' distribution. S refers to the separation point between the two as obtained by finding the split point below which all trials belong to the predictive distribution (red line) and above which all trials belong to the reactive distribution (blue line).

3.3. TFR

The results obtained from the cluster statistical analysis revealed significant differences in TF spectra between the Predictive and Reactive conditions both for data time-locked to the Cue and for data time-locked to participants' response. Regarding the results from the cluster statistical analysis on TF spectra comparing Predictive Vs. Reactive conditions on data time-locked to the Cue and with statistical thresholds set to $\alpha = 0.01$, no significant clusters emerged. Differently, for cluster statistical analysis with thresholds set to $\alpha = 0.05$, one significant cluster emerged between Predictive and Reactive conditions. Fig. 5A shows the significant negative cluster emerged in the β band lasting between 450 ms to 600 ms with respect to the Cue (p-value < 0.05), indicating greater β power in reactive trials in this temporal window.

Regarding the results from the cluster statistical analysis on TF spectra comparing Predictive vs Reactive conditions on data time-locked to participants' response and with statistical thresholds set to $\alpha = 0.05$, one significant cluster emerged between Predictive and Reactive conditions. Fig. 5B shows the significant negative cluster emerged in the β band lasting between −500 ms to −325 ms with respect to participants' response (p-value <0.05), confirming the presence of greater β power in reactive trials during the SET period.

Regarding the results from the cluster analysis on TF spectra comparing Predictive vs Reactive conditions on data time-locked to participants' response and with statistical thresholds set to $\alpha = 0.01$, significant differences emerged between Predictive vs Reactive conditions in all frequency bands investigated. Fig. 6A shows the significant negative cluster in the θ band lasting between −260 ms to 15 ms with respect to participants' response (p-value < 0.01), indicating stronger θ power in reactive trials before response. Fig. 6B shows the significant

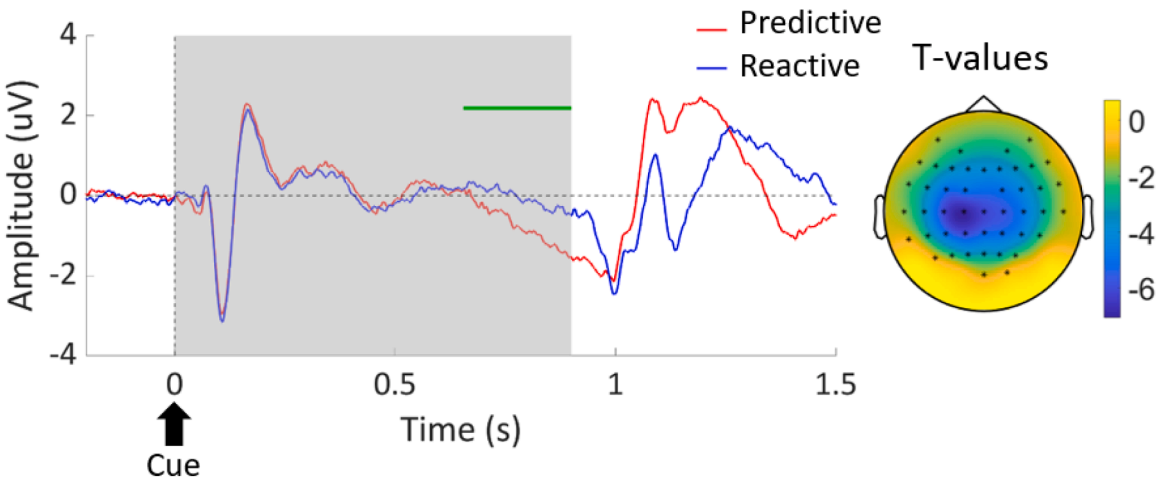


Fig. 3. Significant negative cluster from cluster statistics comparing ERPs in the predictive vs reactive conditions for data time-locked to cue onset. The gray shaded area shows the time of interest for computing the statistics (0 to 900 ms around yellow cue presentation). The green line shows the latency of the significant cluster. The topoplot shows the t-values and the asterisks indicate the channels belonging to the significant cluster. ERPs for the predictive and reactive conditions are separately averaged across the channels belonging to the significant cluster highlighted in the topoplot.

positive cluster in the θ band lasting between 60 ms to 500 ms (p-value < 0.0001), indicating stronger θ power in predictive trials after response. Fig. 6C shows the significant positive cluster in the α band lasting between 85 ms to 210 ms (p-value < 0.0001), indicating stronger α power in predictive trials around participants' response. Fig. 6D shows the significant negative cluster in the β band lasting between 180 ms to 500 ms (p-value < 0.01), indicating stronger β power in reactive trials after response. Fig. 6E shows the significant negative cluster in the γ-band lasting between −50 ms to 30 ms (p-value < 0.01), indicating stronger γ power in reactive trials around response.

4. Discussion

This study aimed to investigate the neural correlates underlying Predictive vs. Reactive strategies in a "starting block" scenario using EEG. We aimed to directly contrast internally-driven (Predictive) vs. externally-driven (Reactive) actions without relying on external manipulations to induce these different behaviors. Unlike previous research that often contrasted top-down and bottom-up strategies with complex tasks that impose different cognitive loads (e.g., higher memory, attentional demands, or conflict processing) for internally-driven actions (Deiber et al., 2012; Obhi et al., 2012; Passingham et al., 2010), our paradigm provided a more naturalistic, balanced comparison of these behaviors by allowing participants to rely on a given strategy (Predictive or Reactive) on a trial-by-trial basis without any external manipulations. Although learning plays a crucial role in optimizing response times by familiarizing participants with the fixed cue-to-target interval, the increase in predictive behavior across experimental blocks cannot be solely attributed to general learning effects. Instead, it reflects the adoption of a distinct cognitive strategy — the predictive strategy. Once participants have learned the fixed relationship between the cue and target, they are able to rely on internally driven predictions about the target onset. Importantly, we know from previous work that when no fixed relationship exists between the cue and target, we do not observe the bimodal distribution in the data that is central to our analysis (Tagliaferri et al., 2023). The early peak of response times is too early (< 170 ms) to be compatible with any physiological bottom-up stimulus-response association (Tagliaferri et al., 2023). Taken together, this indicates that the early peak of RTs is not a result of general performance improvement through practice, (which would apply in all simple RT tasks), but rather of the emergence of a distinct strategy due to the implicit learning of the regularity and predictability of the cue-target temporal interval. Such a regularity allows the participants to adopt the predictive modality. Importantly, the two strategies are not mutually compatible in the same trial and therefore represent the result of a winner-take all neural process. Our EEG findings support this distinction, showing that predictive and reactive behaviors are underpinned by distinct neural mechanisms. Specifically, the contrast between predictive and reactive trials suggests that once the predictive strategy becomes available (through learning the fixed cue-target relationship), it engages top-down, internally driven processes, while reactive behavior remains reliant on externally driven, bottom-up processes.

Importantly, we analyzed EEG data time-locked to both the cue and the motor response in order to examine distinct aspects of predictive and reactive strategies. The cue-locked analyses allowed us to explore the temporal evolution of strategy selection during the preparatory SET period, capturing the unfolding neural dynamics leading up to the GO signal. In contrast, the response-locked analyses provided insight into the distinct neural correlates associated with the execution of these strategies at the moment of motor execution. While some overlap exists in interpretation, the cue-locked data primarily reflect the buildup of strategy-dependent preparatory processes (Section 4.2), whereas the response-locked data reveal the culmination of these processes in action execution (Section 4.3).

4.1. Behavioral findings and strategy differentiation

Consistent with prior studies (Cattaneoand Parmigiani, 2021; Tagliaferri et al., 2023), we observed a bimodal distribution of RTs (Fig. 2A). This distribution reflects two distinct strategies: a predictive strategy, where participants anticipated the GO signal based on the Cue-GO interval, and a reactive strategy, where participants waited for the GO signal to respond/react to it. The earlier mode in the RTs' distribution therefore reflects predictive responses, while the second and later mode captures reactive responses.

Crucially, to classify trials objectively, we used a k-means clustering analysis, which successfully differentiated between Predictive and Reactive trials (Fig. 2B). This unsupervised data-driven approach avoided arbitrary RTs cut-offs, offering a more robust method of trials' classification between the two conditions (Predictive vs. Reactive RTs). The results of this procedure support previous findings on participants' RTs distribution in tasks where the temporal relationship between Cue and Go signal is fixed (Cattaneoand Parmigiani, 2021; Tagliaferri et al., 2023).

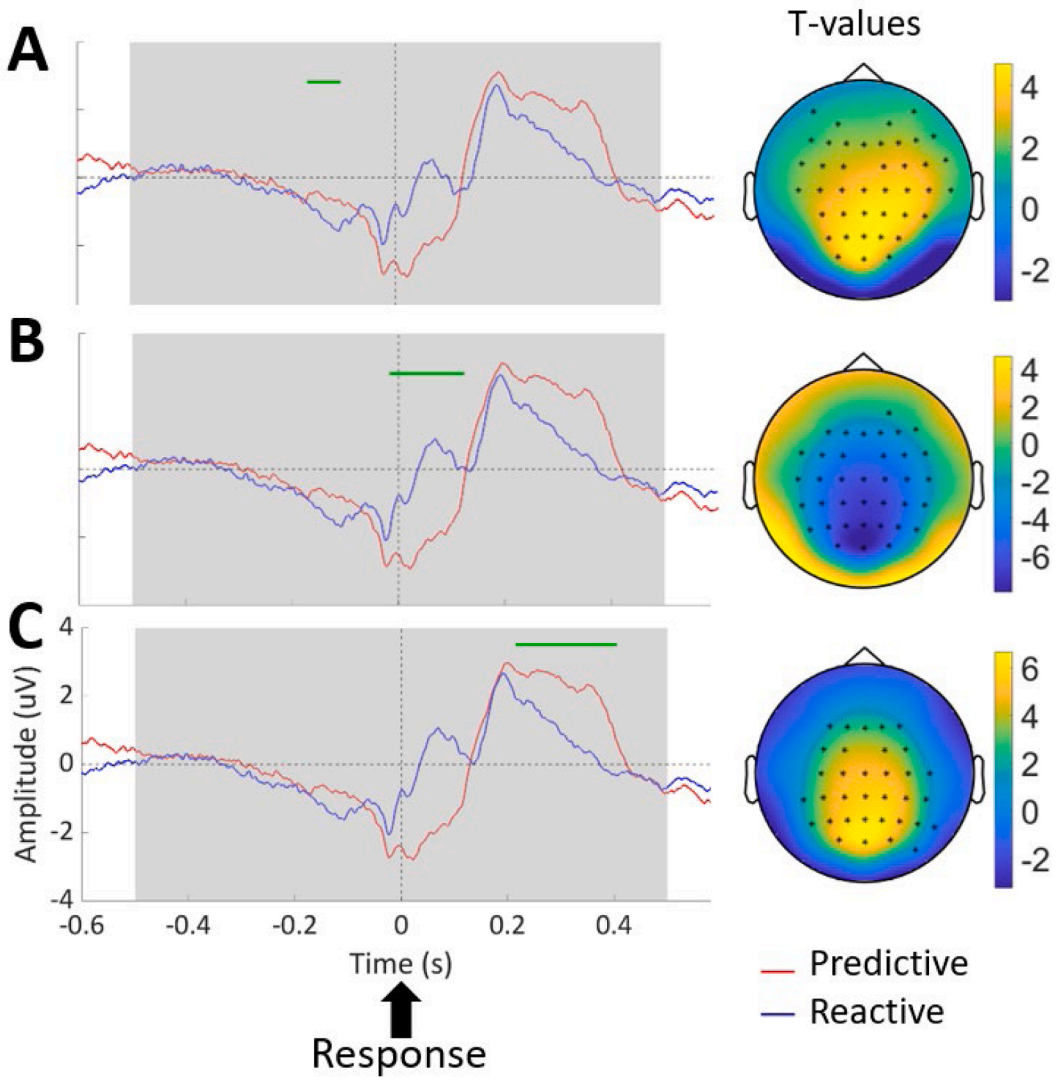


Fig. 4. Significant clusters from cluster statistics comparing ERPs in the predictive vs reactive conditions for data time-locked to the response. The gray shaded area shows the time of interest for computing the statistics for data time-locked to the response (−500 ms to 500 ms around participants' response). The green line shows the latency of the significant cluster. The topoplot shows the t-values and the asterisks indicate the channels belonging to the significant cluster. ERPs for the predictive and reactive conditions are separately averaged across the significant channels highlighted in the topoplot.

4.2. Early EEG activity discriminating predictive and reactive strategies during the SET period

One specific aim of the work was to explore when the neural differences between Predictive and Reactive strategies emerge during the SET period, to find the earliest evidence of strategy choice unravelling. First of all, we observed a significantly deeper contingent negative variation (CNV) following the cue and preceding the GO signal in Predictive compared to Reactive trials (Fig. 3). The CNV is usually considered to be the correlate of accumulator processes occurring in the medial frontal regions, necessary for the internal estimation of time intervals. There is robust multi-layered evidence in the literature that whenever the brain has to count a time interval in the sub-second to multiple-seconds range, the CNV shows up, with a time-course compatible with the behavioral task (Kononowicz and Penney, 2016). Despite not necessarily being a direct correlate of predictive behavior (van Rijn 2011), the CNV is a robust marker of time estimation. This finding is of great importance because it validates the initial assumption that the early responses are based on a time-counting, predictive strategy. As participants rely on internally generated timing mechanisms to optimize their response in Predictive trials, the deeper CNV observed in this condition likely reflects the increased neural resources allocated to calculation of temporal intervals, necessary for temporal anticipation, processes that are known to be associated with the CNV amplitude (Van Rijn et al., 2011; Walter et al., 1964). Therefore, the observation that a CNV was larger in the reactive behavior in comparison to predictive behavior is a very important validation of the fact that the current task is solved by two different strategies with two different underlying neural dynamics.

As for differences in oscillatory dynamics between Predictive and Reactive behavior during the SET period, we found that EEG oscillatory dynamics show differences that appear as early as ~400 ms during the preparatory phase (i.e., ~500 ms before the GO signal) (Fig. 5A, Fig. 5B). Specifically, Predictive trials exhibited lower β power during the SET period and before the GO-signal (Fig. 5A, Fig. 5B), an effect that has been previously associated with temporal prediction, internalized timing processes and, more in general, with modulations due to top-down expectations (Alegre et al., 2003; Forster et al., 2024; Tavano et al., 2019). This previous evidence is therefore in line with our effect of lower β power in Predictive trials, reflecting the engagement of internalized timing processes and top-down mechanisms to anticipate and prepare for the GO signal.

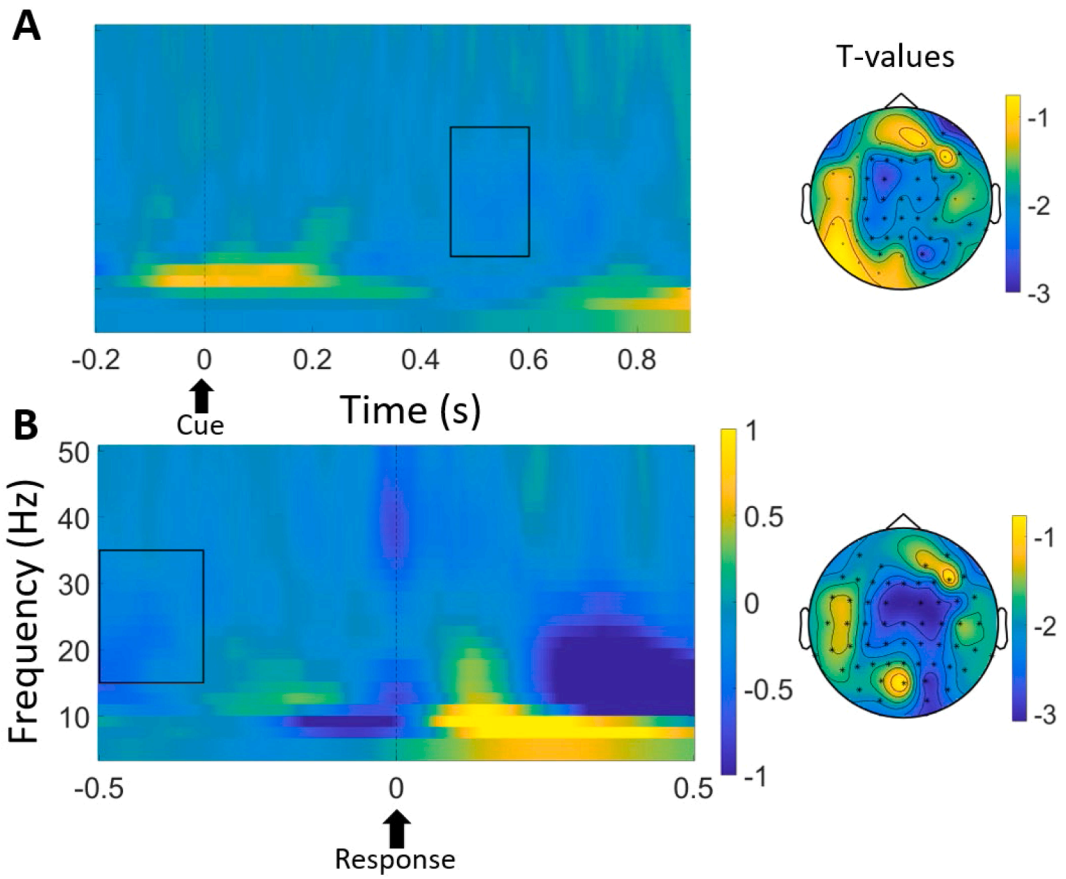


Fig. 5. A) Significant negative cluster in the β band (15–35 Hz) from cluster statistics comparing TF spectra in the predictive vs reactive conditions for data time-locked to cue onset. On the left, the spectrum shows the TF spectral power difference between predictive and reactive conditions as averaged across the channels belonging to the significant cluster highlighted by asterisks in the topoplot. The black rectangle indicates significant frequency band and time points. The topoplot shows the t-values from cluster statistics. Thresholds set to $\alpha = 0.05$ for both the first level and cluster statistics. B) Significant negative cluster in the β band from cluster statistics comparing TF spectra in the predictive vs reactive conditions for data time-locked to response. On the left, the spectrum shows the TF spectral power difference between predictive and reactive conditions as averaged across the channels belonging to the significant cluster highlighted by asterisks in the topoplot. The black rectangles indicate significant frequency band and time points. The topoplot shows the t-values from cluster statistics. Thresholds set to $\alpha = 0.05$ for both the first level and cluster statistics.

Also, α ITPC was stronger in Predictive trials during the same interval of the SET period (Suppl. Fig. 3A), possibly suggesting more consistent engagement of top-down processes during the anticipation of the GO signal (Jensen and Mazaheri, 2010; Lopez et al., 2014; Palva and Palva, 2007; Sauseng et al., 2005).

Interestingly, we found a differentiation between the two strategies that was evident in the second half of the SET period, whatever metrics was applied. With the limitations of a negative finding, we show that at the beginning of the SET period the two strategies were indistinguishable, therefore suggesting that the commitment to one or another strategy builds up during the SET period, and is not the consequence of an early decision. Late neural processes differentiating the two strategies can be interpreted in the light of findings from TMS studies, which demonstrate that, in an identical task as the one used in this work, the two strategies still coexist during the set period and that TMS can still bias individuals toward predictive or reactive strategies when stimulation is given during the second half of the SET period (e.g., Tagliaferri et al., 2023). In this context, the β power and ITPC changes, occurring in the second half of the SET period, probably reflect the gradual buildup of commitment of the participant's brain towards one of the two strategies. One alternative explanation, as discussed by Alegria (1974), is that maintaining a constant state of high readiness from the onset of the SET period may be cognitively costly. In this view, participants might delay full engagement, with neural differences emerging only later in the SET period. While this account is plausible, we consider it unlikely that participants would initiate predictive preparation only in the second half of the SET period. Predictive responses, by definition, rely on precise internal time tracking, which requires continuous monitoring from the start of the SET period. Therefore, the absence of early neural differences may not reflect a lack of early preparation, but rather the gradual and implicit resolution of strategy selection, with both strategies remaining available initially and commitment becoming evident only later in the trial.

4.3. EEG correlates of predictive vs. reactive strategies

While the bimodal distribution of RTs revealed by unsupervised clustering strongly supports the existence of two distinct strategies (Section 4.1), the neural differences reported here are essential to further corroborate these findings. By demonstrating that predictive and reactive strategies are associated with distinct neural correlates, we provide crucial evidence that these strategies represent truly distinct cognitive and neural mechanisms. Across various neural measures—ERPs, TFRs, MI, and ITPC—we found clear differences between these strategies. Although differences were observed in both cue-locked and response-locked data, this section focuses exclusively on response-locked data, which directly reflects the distinct neural correlates of strategy execution at the moment of action.

We observed a significantly larger ERP component, at latencies associated with the P3b, in Predictive trials (Fig. 4). This aligns with the

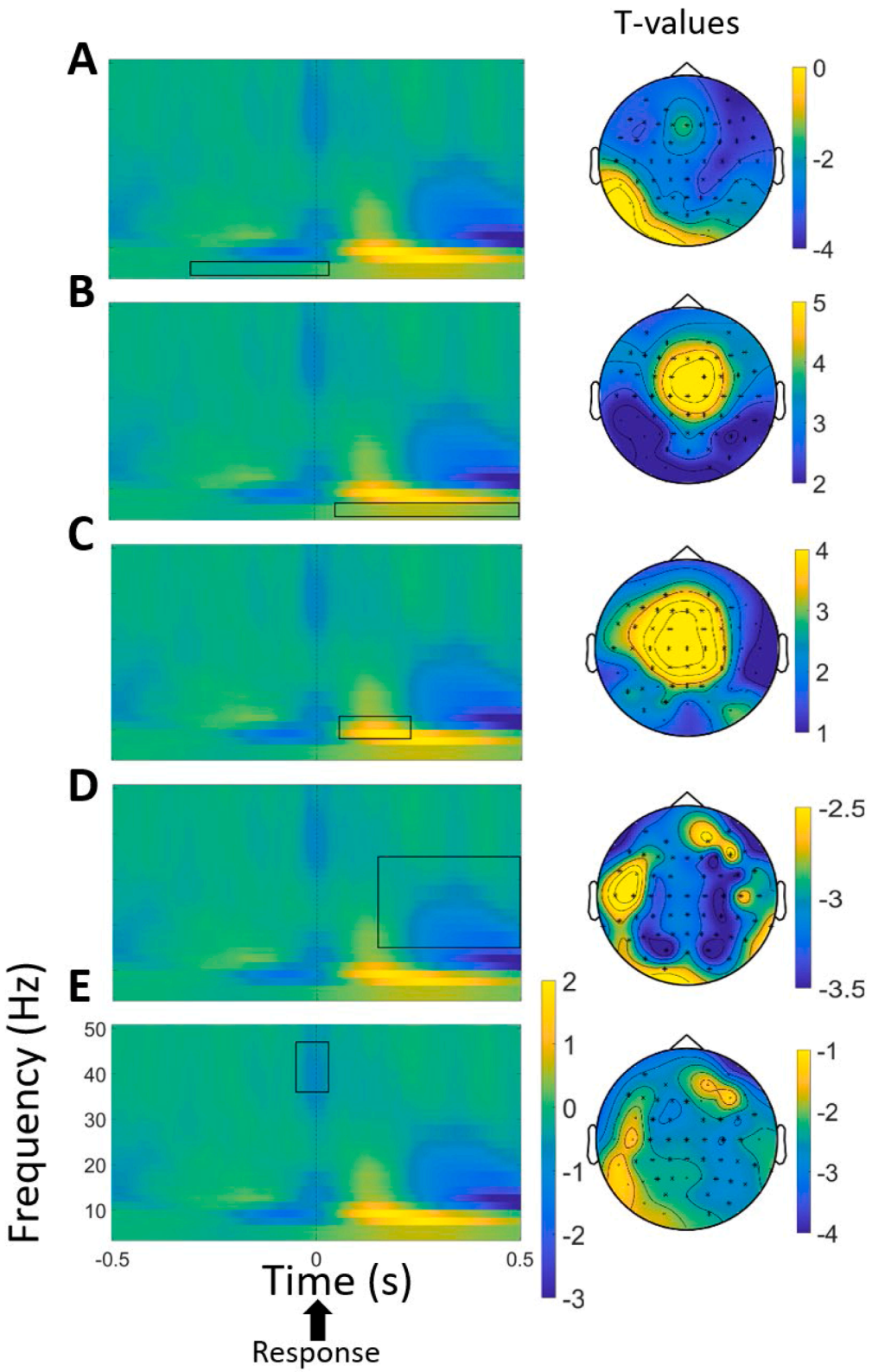


Fig. 6. Significant clusters emerged from the cluster statistics comparing TF spectra in predictive vs reactive conditions for data time-locked around participants' response. On the left, the spectrum shows the TF spectral power difference between predictive and reactive conditions as averaged across the channels belonging to the significant cluster highlighted by asterisks in the topoplot. The black rectangles indicate significant frequency band and time points. The topoplot shows the t-values from cluster statistics. A) Significant negative cluster in θ band with p-value <0.01; B) Significant positive cluster in θ band with p-value < 0.0001; C) Significant positive cluster in the α band with p-value <0.0001; D) Significant negative cluster in the β band (16 – 35 Hz) with p-value< 0.01; E) Significant negative cluster in the γ band with p-value< 0.01. Thresholds set to $\alpha = 0.01$ for both the first level and cluster statistics.

view that temporal prediction is linked to increased amplitude in the P3b component (Hohnsbein et al., 1998; Kok et al., 2001), which reflects cognitive updating processes and prediction error minimization. The larger P3b amplitude observed in Predictive trials likely reflects the brain's updating of internal temporal models based on the learned cue-target interval. This finding is consistent with recent literature, which links the P3b to Bayesian belief updating and surprise processing (Jepma et al., 2018; Kolossa et al., 2015; Mars et al., 2008; Visalli et al., 2023). These studies suggest that the P3b indexes the brain's updating of predictions to minimize prediction error, supporting the notion that the brain uses prior temporal knowledge to prepare for action execution in predictive tasks. This aligns with the idea that adopting a predictive strategy requires integrating temporal cues to anticipate the GO signal, hence engaging higher cognitive control to prepare for action execution.

Further analysis of oscillatory dynamics revealed striking differences in θ, α, β, and γ power comparing Predictive vs. Reactive trials (Fig. 6). Notably, θ power was reduced before motor response and increased after motor response in Predictive trials (Fig. 6A, Fig. 6B). These effects are possibly due to enhanced anticipation of the GO signal and greater monitoring after the response in the predictive strategy, as this pattern is in line with previous works linking θ oscillations to temporal anticipation and cognitive control (Crivelli-Decker et al., 2018; Nigbur et al., 2011). In addition, we observed lower α desynchronization (ERD) and weaker β rebound (ERS) in Predictive trials (Fig. 6C, Fig. 6D), suggesting that participants engaged more effectively in motor preparation and therefore likely required less neural recruitment at the moment of action execution (Deiber et al., 2012). We further extend this finding of more efficient motor planning (in Predictive trials) to the phenomenon of motor-related γ-synchronization which we report to be weaker in Predictive compared to Reactive trials (Fig. 6E). These results indicate that, in conditions where motor preparation is greater (Predictive trials), all three phenomena (α ERD, post-movement β rebound ERS, and γ-ERS) are weakened, potentially due to reduced recruitment of neural assemblies when pre-movement preparation occurs. This result aligns with findings from Jepma et al. (2012), who demonstrated that temporal certainty primarily influences non-decisional processes, such as motor preparation and stimulus encoding, rather than decisional processes. Their study showed that temporal certainty reduces the duration of motor preparation, leading to faster and more efficient responses. In our study, learning the fixed cue-target relationship likely increased participants' temporal certainty, which enabled them to prepare more efficiently, as reflected by alpha, beta, and gamma modulations. These oscillatory changes indicate a boost in motor readiness, helping participants to execute responses more rapidly in the predictive trials.

Taken together, these findings demonstrate neural differences in both ERPs and TFRs that corroborate the existence of two distinct strategies, Predictive and Reactive, as observed in behavioral data. Additional differences in other neural metrics, such as MI and ITPC, further support these results and are detailed in the Supplementary material.

5. Conclusions

This study offers compelling evidence that the early and late responses are characterized by distinct neural dynamics and therefore truly represent two different strategies, Predictive and Reactive. The appearance of a CNV in the early responses is a clear marker of temporal prediction in the early responses, further corroborating the idea of predictive behavior. Specifically, our EEG analyses reveal clear differences in ERPs, TFR, and ITPC between the two conditions. The late emergence of these neural differences during the SET period further suggests that strategy selection is determined by preparatory processes, influenced by modulation of top-down and bottom-up mechanisms. These findings contribute to the growing body of literature on the neural correlates of internally- versus externally-driven actions, capitalizing on a behavioral task in which the two strategies emerge spontaneously, avoiding external manipulations that may introduce confounding cognitive demands and mask the true differences in EEG patterns between conditions.

CRediT authorship contribution statement

Arianna Brancaccio: Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Software, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Marco Tagliaferri:** Writing – review & editing, Software, Methodology, Investigation, Data curation. **Carlo Miniussi:** Writing – review & editing, Writing – original draft, Supervision, Resources, Funding acquisition, Conceptualization. **Luigi Cattaneo:** Writing – review & editing, Writing – original draft, Supervision, Resources, Methodology, Funding acquisition, Conceptualization.

Declaration of competing interest

All authors declare no conflict of interest.

Acknowledgments

This work was supported by the B2B project SPOKE 4. MNESYS grant PNRR – NextGenerationEU.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.neuroimage.2025.121335.

Data availability

The data that support the findings will be available at G-Node GIN (https://gin.g-node.org/arianna.brancaccio/EEG-Dataset-Predictive-vs-Reactive-Behavior.git) following 6 months after project completion.

References

Adams, J.A., Chambers, R.W., 1962. Response to simultaneous stimulation of two sense modalities. J. Exp. Psychol. 63, 198–206.
Adams, J.A., Creamer, L.R., 1962. Anticipatory timing of continuous and discrete responses. J. Exp. Psychol. 63, 84–90.
Alegre, M., Gurtubay, I.G., Labarga, A., Iriarte, J., Malanda, A., Artieda, J., 2003. Alpha and beta oscillatory changes during stimulus-induced movement paradigms: effect of stimulus predictability. Neuroreport 14 (3), 381–385.
Alegria, J., 1974. The time course of preparation after a first peak: some constraints of reacting mechanisms. Q. J. Exp. Psychol. 26 (4), 622–632.
Cattaneo, L., Parmigiani, S., 2021. Stimulation of different sectors of the Human dorsal premotor cortex induces a shift from reactive to predictive action strategies and changes in motor inhibition: a dense transcranial magnetic Stimulation (TMS) mapping study. Brain Sci. 11, 2021, Vol 11, Page 534534–534.
Crivelli-Decker, J., Hsieh, L.T., Clarke, A., Ranganath, C., 2018. Theta oscillations promote temporal sequence learning. Neurobiol. Learn. Mem. 153, 92–103.
Deiber, M.P., Sallard, E., Ludwig, C., Ghezzi, C., Barral, J., Ibañez, V., 2012. EEG alpha activity reflects motor preparation rather than the mode of action selection. Front. Integr. Neurosci. 6, 59.
Forster, C., Stephani, T., Grund, M., Panagoulas, E., Al, E., Hofmann, S.M., … & Villringer, A. (2024). Pre-stimulus beta power encodes explicit and implicit perceptual biases in distinct cortical areas. bioRxiv., 2024-06.
Hohnsbein, J., Falkenstein, M., Hoormann, J., 1998. Performance differences in reaction tasks are reflected in event-related brain potentials (ERPs). Ergonomics 41 (5), 622–633.
Hoshi, E., Tanji, J., 2004. Functional specialization in dorsal and ventral premotor areas. Prog. Brain Res. 143, 507–511.
Jensen, O., Mazaheri, A., 2010. Shaping functional architecture by oscillatory alpha activity: gating by inhibition. Front. Hum. Neurosci. 4, 186.
Jepma, M., Brown, S.B., Murphy, P.R., Koelewijn, S.C., de Vries, B., van den Maagdenberg, A.M., Nieuwenhuis, S., 2018. Noradrenergic and cholinergic modulation of belief updating. J. Cogn. Neurosci. 30 (12), 1803–1820.
Jepma, M., Wagenmakers, E.J., Nieuwenhuis, S., 2012. Temporal expectation and information processing: A model-based analysis. Cognition 122 (3), 426–441.

Kok, A., 2001. On the utility of P3 amplitude as a measure of processing capacity. Psychophysiology 38 (3), 557–577.
Kolossa, A., Kopp, B., Fingscheidt, T., 2015. A computational analysis of the neural bases of bayesian inference. Neuroimage 106, 222–237.
Kononowicz, T.W., Penney, T.B., 2016. The contingent negative variation (CNV): Timing isn't everything. Curr. Opin. Behav. Sci. 8, 231–237.
López, M.E., Garcés, P., Cuesta, P., Castellanos, N.P., Aurtenetxe, S., Bajo, R., Maestú, F., 2014. Synchronization during an internally directed cognitive state in healthy aging and mild cognitive impairment: a MEG study. Age (Omaha) 36, 1389–1406.
Mars, R.B., Debener, S., Gladwin, T.E., Harrison, L.M., Haggard, P., Rothwell, J.C., Bestmann, S., 2008. Trial-by-trial fluctuations in the event-related electroencephalogram reflect dynamic changes in the degree of surprise. J. Neurosci. 28 (47), 12539–12545.
Milloz, M., Hayes, K., Harrison, A.J., 2021. Sprint start regulation in athletics: a critical review. Sports Med. 51, 21–31.
Mita, A., Mushiake, H., Shima, K., Matsuzaka, Y., Tanji, J., 2009. Interval time coding by neurons in the presupplementary and supplementary motor areas. Nat. Neurosci. 4 (12), 502–507, 2009 12.
Niemi, P., Näätänen, R., 1981. Foreperiod and simple reaction time. Psychol. Bull. 89, 133–162.
Nigbur, R., Ivanova, G., Stürmer, B., 2011. Theta power as a marker for cognitive interference. Clin. Neurophysiol. 122 (11), 2185–2194.
Obhi, S.S. (2012). The troublesome distinction between self-generated and externally triggered action: a commentary on Schüür and Haggard.
Oostenveld, R., Fries, P., Maris, E., Schoffelen, J.M., 2011. FieldTrip: open source software for advanced analysis of MEG, EEG, and invasive electrophysiological data. Comput. Intell. Neurosci. 2011, 1–9.
Palva, S., Palva, J.M., 2007. New vistas for α-frequency band oscillations. Trends. Neurosci. 30 (4), 150–158.
Passingham, R.E., Bengtsson, S.L., Lau, H.C., 2010. Medial frontal cortex: from self-generated action to reflection on one's own performance. Trends Cogn. Sci. (Regul. Ed.) 14 (1), 16–21.
Rizzolatti, G., Cattaneo, L., Fabbri-Destro, M., Rozzi, S., 2014. Cortical mechanisms underlying the organization of goal-directed actions and mirror neuron-based action understanding. Physiol. Rev. 94, 655–706.
Sauseng, P., Klimesch, W., Doppelmayr, M., Pecherstorfer, T., Freunberger, R., Hanslmayr, S., 2005. EEG alpha synchronization and functional coupling during top-down processing in a working memory task. Hum. Brain Mapp. 26 (2), 148–155.
Schmidt, R.A., 1968. Anticipation and timing in human motor performance. Psychol. Bull. 70, 631–646.
Shima K., Tanji J. (2000): Neuronal activity in the supplementary and presupplementary motor areas for temporal organization of multiple movements. https://doi.org/10.1152/jn20008442148 84:2148–2160.
Tagliaferri, M., Giampiccolo, D., Parmigiani, S., Avesani, P., Cattaneo, L., 2023. Connectivity by the frontal aslant tract (FAT) explains local functional specialization of the superior and inferior frontal gyri in humans when choosing predictive over reactive strategies: a tractography-guided TMS study. J. Neurosci. 43, 6920–6929.
Tavano, A., Schröger, E., Kotz, S.A., 2019. Beta power encodes contextual estimates of temporal event probability in the human brain. PLoS One 14 (9), e0222420.
Ullsperger, P., Metz, A.M., Gille, H.G., 1988. The P300 component of the event-related brain potential and mental effort. Ergonomics 31 (8), 1127–1137.
Van Der Steen, M.C., Keller, P.E., 2013. The adaptation and anticipation model (ADAM) of sensorimotor synchronization. Front. Hum. Neurosci. 7. https://doi.org/10.3389/fnhum.2013.00253.
Van Rijn, H., Kononowicz, T.W., Meck, W.H., Ng, K.K., Penney, T.B., 2011. Contingent negative variation and its relation to time estimation: a theoretical evaluation. Front. Integr. Neurosci. 5, 91.
Visalli, A., Capizzi, M., Ambrosini, E., Kopp, B., Vallesi, A., 2023. P3-like signatures of temporal predictions: a computational EEG study. Exp. Brain Res. 241 (7), 1919–1930.
Walter, W., Cooper, R., Aldridge, V., et al., 1964. Contingent negative variation: an electric sign of sensori-motor association and expectancy in the Human brain. Nature 203, 380–384. https://doi.org/10.1038/203380a0.

Further reading

Michelet, T., Duncan, G.H., Cisek, P., 2010. Response competition in the primary motor cortex: corticospinal excitability reflects response replacement during simple decisions. J. Neurophysiol. 104, 119–127.
Schubotz, R.I., 2007. Prediction of external events with our motor system: towards a new framework. Trends Cogn. Sci. 11, 211–218.
Toni, I., Schluter, N.D., Josephs, O., Friston, K., Passingham, R.E., 1999. Signal-, set- and movement-related activity in the Human brain: an event-related fMRI study. Cereb. Cortex. 9, 35–49.
Van Der Cruijsen, J., Manoochehri, M., Jonker, Z.D., Andrinopoulou, E.R., Frens, M.A., Ribbers, G.M., Selles, R.W., 2021. Theta but not beta power is positively associated with better explicit motor task learning. Neuroimage 240, 118373.