

The spectral dynamics of visual awareness: An interplay of different frequencies?

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Funding information

Fondazione Cassa di Risparmio di Verona
Vicenza Belluno e Ancona: Ricerca
scientifica d'eccellenza 2018,
Grant/Award Number: 2018.0861;
Ministero dell'Istruzione, dell'Università e
della Ricerca, Grant/Award Number:
2017TBA4KS_002

Edited by: Christoph M. Michel

Abstract

The goal of this study was to investigate the neurophysiological correlates of visual awareness, with a specific focus on its event-related spectral perturbation (ERSP) features. To this aim, we tried to disentangle the proper neural correlates of consciousness (NCC) from other prerequisite and post-perceptual processing. To do so, we administered an orientation discrimination task, inducing a response bias through task instructions. EEG results showed that different frequency bands are involved in this kind of task, with different spectral and temporal dynamics. In particular, alpha and beta bands seem to be particularly engaged, especially in the aware-unaware contrast, showing a main power suppression for aware trials and replicating previous literature. Moreover, we demonstrated that the process of visual awareness is orchestrated by a complex interaction of different frequencies (i.e., theta, alpha, beta and gamma) being involved as prerequisites and post-perceptual processes.

KEYWORDS

decision bias, ERSP, NCC, visual awareness

1 | INTRODUCTION

One of the most studied topics in neuroscience concerns how consciousness arises. Neural correlates of consciousness (NCC) are defined as the minimal set of neural mechanisms needed for a conscious experience or percept (Koch & Crick, 2004). A helpful technique to shed light on NCC by highlighting their temporal dynamics and spectral features is electroencephalography (EEG). In this framework, visual awareness has been largely investigated, especially through the analysis of the event-related potentials (ERPs), which provide high temporal precision and accuracy in characterising the brain's response to a stimulus. Moreover, another analysis that may unveil the temporal dynamics of these perceptual processes is the study of event-related spectral

perturbation (ERSP). This analysis has the advantage of shedding light on the time and frequency features of the EEG signal and may help to understand the mechanisms through which consciousness is achieved, as it has been previously suggested that different frequency bands can have different roles in neural processing (Fries, 2005).

Despite an extensive investigation, the identification of a proper NCC is still an open issue. Indeed, it remains challenging to disentangle the specific NCC contribution to awareness from the prerequisites of conscious perception and its post-perceptual processes (Pitts et al., 2014).

Specifically, different ERP studies suggested two possible correlates for visual awareness: visual awareness negativity (VAN), an early component occurring around 200 ms after stimulus presentation on occipito-temporal sites, and late positivity (LP), a component with a later

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latency (about 300–500 ms after stimulus presentation) and mainly distributed over central regions (Koivisto & Revonsuo, 2003, 2010). Despite the identification of these two components, it is still unclear whether one of them is the specific NCC, namely the LP component, which could instead reflect post-perceptual processes (Pitts et al., 2014). In a study conducted by Mazzi et al. (2020), the response criterion was manipulated in order to unravel the difference between visual awareness and post-perceptual processes. Indeed, shifting the response criterion across conditions (e.g., from a liberal to a conservative criterion) allows for modulating how a percept is translated into a response. This means that if there is a modulation in the ERP, this would reflect other post-perceptual processes in addition to the sole correlate of visual awareness. For example, in a previous study with a forced-choice detection task, participants were asked if they had seen or not a stimulus, and then they were asked to rate their confidence according to a four-point scale (Ye & Lyu, 2019). The authors found that only the P3 component (in the same temporal window as LP) was modulated by confidence levels, whereas the early component in the N1–N2 temporal window (i.e., VAN) was not influenced by confidence levels, hence probably representing an early correlate of visual awareness. The findings suggested that the VAN reflects the proper marker for the emergence of visual awareness, whereas the LP represents the involvement of post-perceptual processes, in agreement with evidence from previous studies (Koivisto & Grassini, 2016; Wilenius-Emet et al., 2004).

Concerning the studies conducted on ERSP, mixed findings have emerged. In this respect, a frequency band that has been previously correlated with awareness is the gamma frequency (from 30 Hz above). For instance, a previous study found a strong modulation of gamma frequencies in response to perceived stimuli (i.e., faces), which interested occipital, parietal and temporal sites and suggested that gamma may also play a role in the coordination of different brain regions (Lachaux et al., 2005). Another study recorded intracranial activity, whereas epileptic patients were administered a backward masking task and reported an increase in gamma power for successful recognition (Fisch et al., 2009). On the other hand, another study investigating NCC with a metacontrast paradigm found that awareness was associated with less gamma power over the occipital cortex (Aru & Bachmann, 2009). This finding seemed to be in contrast with the others previously reported. However, the authors suggested that the apparent inconsistency may be explained by the presence of a mask in their metacontrast paradigm, which replaced the target in working memory and led to stronger mask processing.

Moreover, with the aim to disentangle NCC from pre- and post-perceptual processes, Aru, Bachmann, et al. (2012) administered a task in which they manipulated not only the sensory evidence of the stimuli presentation (images at different levels of degradation with high or low noise) but also the exposure to the task-related stimuli before the test phase. The authors predicted that the neural processes reflecting conscious perception should be modulated by both factors. However, they found the effect of sensory evidence translated into an enhancement of the gamma band for a higher proportion of seen trials, but the previous exposure to the images had no effect on gamma. Therefore, they suggested that since the gamma band was only correlated with sensory evidence, it may not reflect the proper correlate of conscious perception.

The quest for the NCC becomes more complex considering the evidence from other studies investigating mainly alpha frequencies (8–14 Hz). Indeed, different studies found an association between alpha and visual processing, reporting that reduced alpha power correlates with a higher awareness or detection rate of visual stimuli (Benwell et al., 2017; Mathewson et al., 2009; Samaha et al., 2017). Moreover, the alpha phase has been linked to visual awareness, suggesting that the phase may correspond to different degrees of cortical excitability. This means that stimuli presented at specific moments of the alpha cycle may be more or less likely to be detected, depending on the fluctuations of cortical excitability (Mathewson et al., 2009, 2011).

It is noteworthy to report that studies investigating ERSP often select a priori frequency bands for their analysis (e.g., Aru, Axmacher, et al., 2012; Aru & Bachmann, 2009; Mathewson et al., 2009). Investigating a broader space of frequencies can give a more complete picture of the bands involved in visual processing. For example, Lachaux et al. (2005) found a stronger modulation of gamma when participants perceived the stimuli, but they also found a decrease in alpha and beta bands occurring during the increase of gamma. Nonetheless, the theoretical debate still remains open, as it is difficult to disentangle conscious perception from the prerequisites of consciousness or post-perceptual processing (see Aru, Bachmann, et al., 2012; De Graaf et al., 2012, for a review).

With the same logic adopted by Mazzi et al. (2020), Kloosterman et al. (2019) also investigated how participants' responses are influenced by the criterion. Specifically, they asked participants to report whenever they perceived a target hidden among a continuous stream of visual patterns, and the authors manipulated participants' decision criterion by differently penalising missed and false alarm targets. In this way, when participants were penalised after missing targets, they adopted a more liberal criterion, whereas when they were penalised after

false alarms, they shifted their criterion towards a more conservative one. The authors found that the liberal criterion was associated with a stronger response of pre-stimulus theta power over midfrontal regions and with a pre-stimulus suppression of alpha power over posterior sites that triggered an increase in gamma, suggesting that the decision bias is flexibly adjusted through visual cortex excitability.

The aim of the present paper is twofold: (1) to investigate the spectral dynamics of visual awareness by taking a broader approach and analysing different frequency bands, and (2) to understand if and how these frequency bands are influenced by response criterion. To do so, we asked participants to perform an orientation discrimination task with different instructions, following a conservative, liberal or natural personal response criterion.

2 | METHODS

The methods of the present work have already been described by Mazzi et al. (2020). Data were recorded in two different experimental sessions. In the first one, participants were asked to respond with a conservative and a liberal criterion in two separate series of blocks. In the second one, carried out some months later, participants were asked to respond with their natural internal criterion.

3 | PARTICIPANTS

We initially recruited 59 right-handed participants with normal or corrected-to-normal vision who were naive as to the purpose of the study. After the threshold assessment designed to select the stimuli for the subsequent EEG experiment, 21 participants were not included in the sample: six were not able to modulate the response criterion (conservative and liberal psychometric functions were overlapped), 12 did not show any modulations of stimulus awareness as a function of the spatial frequency (at least one of the two psychometric functions was flat), and three were discarded because, at least in one of the two criteria, the whole psychometric function was above the 50% level. Although high, this participant exclusion rate is not unusual in this kind of psychophysical thresholding procedure. Of the 38 remaining participants who performed the main experiment, four were further excluded due to EEG recording issues, one was discarded because it showed the opposite response bias shift, and nine were excluded because the difference between conservative and liberal awareness was less than 10%. Finally, eight participants who took part in the first conservative and liberal session dropped out of the study due

to time constraints. A total of 16 participants (9 females, mean age = 21.8 years, range = 19 to 25) were thus included in the present work, as they agreed to participate in a second session assessing the natural response criterion. All of them were right-handed with normal or corrected-to-normal vision. They were recruited from the University of Verona, and all of them signed informed consent before taking part in the study and were reimbursed for their participation. The experiment was approved by the local ethics committee and conducted in accordance with the guidelines of the Declaration of Helsinki (World Medical Association, 2013).

3.1 | Stimuli and procedure

First of all, each participant underwent a threshold assessment procedure to select the individual threshold for the main experimental session, defined as the stimulus yielding 50% of aware responses. Visual stimuli consisted of Gabor patches with either a vertical or horizontal orientation and with 4° of visual angle (Michelson contrast: 0.50). Catch trials were defined as Gabor patches with a plaid pattern (spatial frequency of 4.5 c/deg). For this test phase, participants were presented with seven preselected vertical and horizontal spatial frequencies (4.5, 5.0, 6.0, 6.5, 7.0, 7.5 and 8.5 c/deg), and they were asked to respond by pressing a numeric key on the computer keyboard if the orientation of the stimulus was vertical (key 1), horizontal (key 2) or not recognised (key 0). The stimuli appeared for 35 ms at the top centre of the screen (11° above the fixation cross) on a grey background (3.9 cd/m²) and were presented on a 17-in. CRT monitor (LG L1753HM, resolution 1024 × 768 pixels, refresh rate 85 Hz) placed 57 cm away from the participant's eyes. The stimuli were generated by MATLAB custom code (The Mathworks Inc., Natick, MA, USA) and displayed through E-prime 2.0 software (E-Prime Psychology Software Tools Inc., Pittsburgh, PA, USA) running on a Windows operating system, which was also used to collect behavioural data. Before starting the data collection, the timing of the event markers and the effective duration of the stimuli were verified by means of a photodiode and an oscilloscope.

Participants sat in a dimly lit room and had their heads supported by a chinrest. The threshold assessment was performed consecutively for the conservative and liberal criteria (the order of the two criteria was counterbalanced across participants). In the conservative session, participants were asked to respond only if they clearly perceived the orientation of the stimulus, whereas in the liberal session, they were asked to respond even if they had a minimal impression of the orientation. Each

threshold assessment included six blocks of 77 trials for a total of 462 trials (for each of the seven spatial frequencies and the two orientations, there were 30 experimental trials and 42 catch trials). Finally, the psychometric function for each of the response criteria was computed, and the means between the conservative and liberal horizontal threshold values and the conservative and liberal vertical threshold values were used, respectively, as the spatial frequency of the target stimuli for the main task.

The main experimental session was similar to the threshold assessment, but only two kinds of near-threshold stimuli (vertical or horizontal) were presented. The instructions for the induced response criterion were the same as in the threshold procedure, and for the natural response criterion, participants were given no instruction on how to respond (data from the conservative and liberal sessions were collected on the same day, whereas the natural session was conducted in a second moment). Each experimental session included six blocks of 77 trials, with a total of 462 trials (210 horizontal, 210 vertical and 42 catch trials). The trial sequence started with a fixation cross positioned at the centre of the screen and lasting 400 ms, followed by an auditory warning signal at 1000 Hz lasting 150 ms and a random interval (all possible values ranging from 300 to 500 ms) before the target presentation (35 ms). Participants had until 2500 ms to give an answer, and after their responses, a new trial started (see Figure 1a).

3.2 | EEG recording

While participants were engaged in the task, the continuous EEG signal was recorded through BrainAmp amplifiers (Brain Products GmbH, Munich, Germany–Brain Vision Recorder) from 59 Ag/AgCl electrodes mounted on an elastic cap (EasyCap, GmbH, Herrshing, Germany), placed according to the 10–10 international system. We recorded electrooculographic (EOG) activity by means of additional electrodes placed around the eyes (lateral canthi and above and below the right eye). Electrode AFz served as the ground and the right mastoid (RM) as the online reference. Electrode impedance was set below 5 K Ω . Data were recorded at a sampling rate of 1000 Hz with a time constant of 10 s as a low cut-off and a high cut-off of 250 Hz.

4 | DATA ANALYSIS

4.1 | Behavioural data

A detailed description of the behavioural data analysis and results can be found in our previous study (Mazzi et al., 2020). Briefly, the analysis included only trials where a response was provided and with reaction times higher than 150 ms and lower than 1500 ms. The mean percentage of aware and unaware trials was calculated

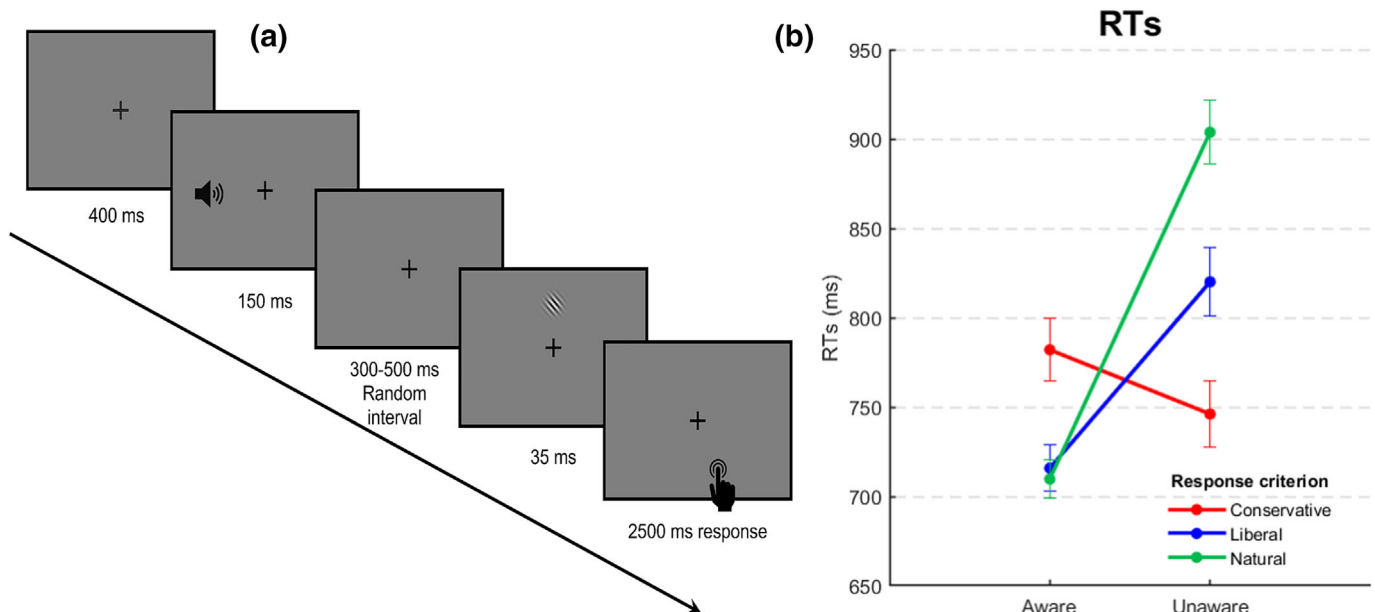


FIGURE 1 Example of the experimental paradigm and behavioural results. (a) Panel A shows an example of the experimental paradigm. The trial began with a fixation cross at the centre of the screen that lasted 400 ms, followed by a warning tone (150 ms) and a random interval (300–500 ms). After that, the target was presented at the spatial frequency selected for each participant according to the threshold assessment procedure and lasted 35 ms. Participants had up to 2500 ms to provide an answer by pressing a key (key 1 if they saw a vertical orientation, key 2 for a horizontal orientation, and key 0 if they were not aware of the orientation). (b) Panel B shows the mean response times (RTs) for aware and unaware trials in all the response criteria (conservative in red, liberal in blue and natural in green).

for each of the response criteria. Significance testing was assessed by means of a 2×3 repeated measures ANOVA.

4.2 | EEG pre-processing and analysis

The analysis of EEG data was performed using MATLAB (version 2020b; The MathWorks, Inc., Natick, MA) scripts and functions from the EEGLAB toolbox (version 2020.0; Delorme & Makeig, 2004). Data were filtered off-line using a zero-phase Hamming windowed sinc FIR high-pass filter at 0.1 Hz (cut-off frequency $[-6$ db]: .05 Hz, transition bandwidth: 0.1 Hz) and a low-pass filter at 80 Hz (cut-off frequency $[-6$ db]: 90 Hz, transition bandwidth: 20 Hz). Line noise was removed through a notch filter (cut-off frequencies: 49.5 and 50.5 Hz, transition bandwidth: 1 Hz). After that, we downsampled the data at 250 Hz, and we detected artifactual EEG channels by means of the `clean_channels` function, using a correlation criterion of 0.5 (for the conservative session, this criterion led to the exclusion of 0.94 channels on average, $SD = 1.18$, range = $[0$ 4]; for the liberal session, 1.06 channels on average, $SD = 1.34$, range = $[0$ 4]; for the natural session, 0.75 channels on average, $SD = 0.68$, range = $[0$ 2]). In order to provide the independent component analysis (ICA) algorithm with a cleaner dataset and simplify the identification of artefacts, we applied a stronger preprocessing (Winkler et al., 2015). Specifically, we filtered the dataset with a high-pass filter at 1 Hz, we epoched from -1350 to 2000 ms with respect to stimulus onset, avoiding overlap between epochs, and we detected and removed artifactual epochs by means of improbability and kurtosis criteria ($SD > 5$ for single channels and $SD > 3$ for global threshold). After that, we computed ICA using the FastICA algorithm (Hyvarinen, 1999) through the TESA toolbox (Rogasch et al., 2017), and we corrected for blinks, eye movements and muscular activity based on the scalp topography, time course and power spectrum of the components. The ICA weights and solutions were applied to the original dataset that was also segmented into longer epochs, from -1850 to 2500 ms. Afterward, removed channels were interpolated by means of the spherical spline algorithm (Perrin et al., 1989), data were re-referenced to average, and linear baseline correction was applied from -300 to 0 ms to help carry out the following preprocessing steps, removing offset. Subsequently, we removed bad epochs based on extreme value thresholds (± 100 μ V), improbability and kurtosis criteria ($SD > 5$ for single channel and $SD > 3$ for global threshold), and abnormal trends in the data (maximum slope allowed = 50 μ V, and minimal R squared allowed = 0.3). This procedure was implemented by means of the trial-by-trial (TBT) plugin of EEGLAB,

which allows the rejection and interpolation of channels on a trial-by-trial basis. If an epoch had more than six channels with artifactual signals, it was removed, whereas if this criterion was not met, the channels were interpolated. Further analysis was performed only on epochs corresponding to responses with a response time (RT) < 1500 and > 150 ms (because these trials were not also considered for the behavioural analysis). Therefore, the average number of epochs included in the analysis was 176.02 for aware conservative, 213.81 for unaware conservative, 279.25 for aware liberal, 106.31 for unaware liberal, 307.44 for aware natural and 89.06 for unaware natural. Unaware trials corresponded to a response of 'not recognised' (key 0), and aware trials were considered irrespective of the accuracy of the response.

4.3 | Time-frequency analysis

To compute time-frequency analysis, we used the `newtimef` function implemented in the EEGLAB toolbox (version 2020.0; Delorme & Makeig, 2004). We extracted ERSP (in dB) considering the frequency from 4 to 80 Hz (linearly spaced with 1 Hz resolution) and using wavelets with a length of 836 ms. These wavelets increase the number of cycles as a function of the frequency to allow a good trade-off between the frequency and temporal resolution (min number of cycles = 3, max number of cycles = 40). The average power of the entire epoch was used as a baseline (Cohen, 2014), which was applied with a full-epoch single-trial normalisation (i.e., divisive method; Grandchamp & Delorme, 2011) to avoid biases due to the use of a pre-stimulus baseline. Firstly, ERSP was extracted for every single condition (aware and unaware in each response criterion). Then, to test for the main effect of the awareness factor, the average of the ERSPs for the aware responses in the three response criteria and the average of the ERSPs for the unaware responses in the three response criteria were computed, whereas to test for the main effect of the criterion factor, the average between aware and unaware ERSPs was computed separately for each response criterion. Statistical differences for the interaction and the main and simple effects were tested by means of the threshold-free cluster-enhancement (TFCE) method, which improves the detection of diffuse, low-amplitude signals and allows non-parametric correction for multiple comparisons with a permutation test ($p < 0.05$; for details, see Smith & Nichols, 2009). This approach has been shown to successfully control type I error and has the advantage of moving beyond the thresholding criticism about classical cluster-based approaches by avoiding a priori assumptions about data. The chosen number of permutations was 2000,

whereas values for the parameters E and H were set at 0.66 and 2, respectively. Statistical tests were applied for each sample of the 59 EEG channels, each of the 176-time points (a time window from -1432 to 2068 ms with a resolution of about 20 ms), and each of the 77 frequencies (range: 4–80 Hz).

5 | RESULTS

5.1 | Behavioural results

To support the understanding of time-frequency results, we decided to report here the main findings of the RT analysis (Figure 1b). For a detailed description of the results, refer to Mazzi et al. (2020). There was no significant effect of the criterion factor. The effect of awareness was translated into faster RTs for aware trials as compared with the unaware. The interaction between

awareness and criterion was also significant, and when further investigated through post-hoc pairwise comparisons, it emerged that there were significant differences in the unaware trials between the conservative and liberal criteria and between the conservative and natural criteria. No significant difference was found in the liberal vs. natural contrast.

5.2 | EEG results

Concerning the main effects, we did not find any significant difference in the response criterion factor. However, for the awareness effect, results showed different significant clusters. For the purposes of this paper, we will focus on the effects found between -200 and 800 ms, respectively, before and after stimulus presentation. Figure 2a represents a schematic depiction of the results for the main effect, where each row represents an average

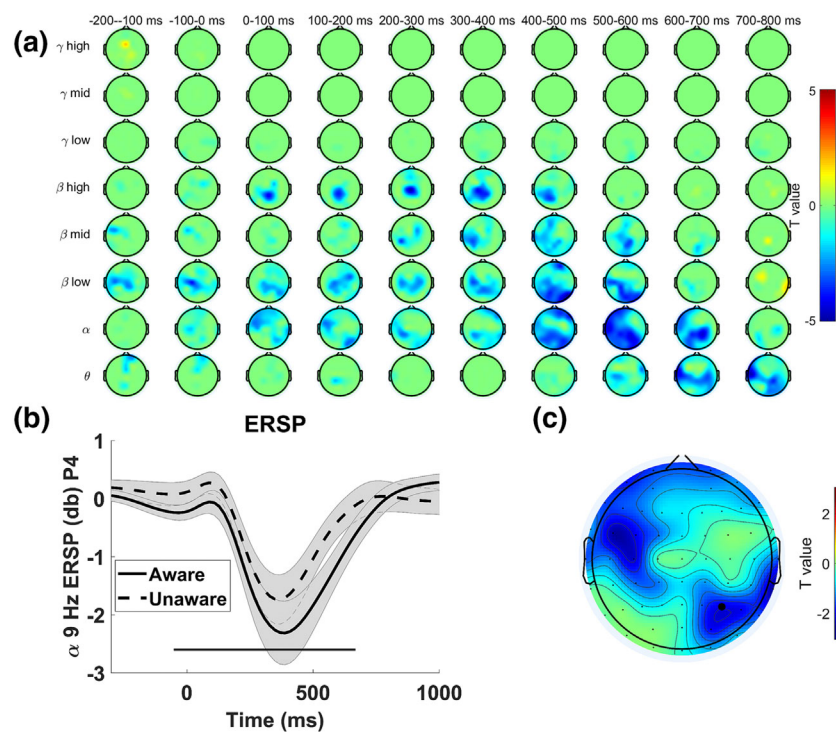


FIGURE 2 Results of the awareness effect for the scalp-based time-frequency analysis. (a) Panel A shows the topoplots for the results of the main effect of awareness. Each row represents the average of each frequency band (specifically, theta: 4–7 Hz, alpha: 8–13 Hz, beta1: 14–19 Hz, beta2: 20–25 Hz, beta3: 26–30 Hz, gamma1: 31–45 Hz, gamma2: 46–65 Hz and gamma3: 66–80 Hz), and each column represents the average of electroencephalography (EEG) significant clusters every 100 ms from 200 ms before stimulus presentation up to 800 ms after its onset. The topoplots show only the t values of the significant results after threshold-free cluster-enhancement (TFCE). Please note that the average on frequency bands and time bins is used only for illustrative purposes and that the analysis was conducted on each channel, frequency and time point. (b) Panel B shows the event-related spectral perturbation (ERSP) traces for the results of the simple effect of the awareness factor. The solid (aware trials) and dashed lines (unaware trials) show representative data for a frequency in the alpha band (9 Hz) extracted from channel 15 (P4). The black line below highlights the temporal window in which this effect was significant. Shaded areas show the standard error. (c) Panel C shows the topoplot computed as the average of the significant results between 8 and 13 Hz in a representative temporal window from 0 to 300 ms. The bold black dot represents the channel plotted in the ERSP (P4).

of each frequency band, and the columns represent an average every 100 ms from -200 to 800 ms. Please note that the average on frequency bands and time bins is used only for illustrative purposes and that the analysis was conducted on each sample of channel, frequency and time point. For descriptive purposes, we will refer to the set of closely significant points as a 'cluster'.

We found a small cluster for theta frequencies (4–7 Hz), mainly interesting frontal channels, from around 200 ms before stimulus presentation until its onset. Later in time, starting around 400 ms after the stimulus, we found a bigger cluster engaging more channels over the scalp (over the frontal, central and posterior regions). Both effects were due to a stronger suppression in the aware trials as compared with the unaware trials.

Concerning alpha frequency (8–12 Hz), we found a main significant cluster starting about 100 ms before the stimulus presentation and spreading over the left centro-frontal and right occipital regions as time passed. Around 400–600 ms, this cluster interested almost all regions over the scalp, and it started diminishing again around 700 ms. All these effects were due to a more reduced alpha power for aware than unaware trials (see Figure 2b,c for an example).

Furthermore, an activity of low beta frequencies (14–19 Hz) was evident already from 200 ms before the stimulus and localised over the left centro-temporal regions. After stimulus presentation, significant clusters were mainly evident over the central, right parietal and frontal regions, until around 400–500 ms, when significant clusters spread over the posterior and right frontal channels, to disappear around 600–800 ms. This effect was due to a stronger event-related suppression of power for aware trials as compared with unaware trials. Mid- and high-beta frequencies (20–30 Hz) were mainly involved after stimulus presentation. Significant clusters mainly engaged central channels (especially for high beta frequencies) from stimulus presentation until around 400–500 ms, whereas mid-beta showed an involvement mainly around 300–400 ms interesting left central channels, gradually spreading over more posterior and frontal channels as time passed, until about 500–600 ms. Similar to the previous frequencies' bands, these effects were characterised by a stronger event-related suppression of power for aware trials.

Low gamma frequencies were only moderately involved, especially between 31 and 33 Hz. This cluster was found from around stimulus presentation until about 600 ms after its onset. It interested the central and frontal regions and was mainly due to a stronger power reduction for aware trials as compared with unaware trials. This cluster interested fewer channels, mainly over the occipital regions, and was found later in time (around

500–800 ms) as frequencies increased and completely disappeared after around 40 Hz.

Mid- (from 60 Hz) and high-gamma frequencies showed a significant cluster localised mainly over central channels and present until around the presentation of the stimulus. This effect was mainly due to an opposite pattern between aware and unaware trials, as the power of the aware was higher and the power of the unaware was reduced.

To obtain the interaction effects, we tested the visual awareness effect, computed as the difference between aware and unaware trials, across the three response criteria. We found different significant clusters (Figure 3a represents a schematic depiction of the results of the interaction). Indeed, results from the interaction revealed a first involvement in time of all beta frequencies from around 100 ms before stimulus presentation, interesting channels mainly over left mid-temporal sites. In low beta, this cluster gradually spread over more occipital and central regions as time passed (until 800 ms after stimulus presentation), whereas upper beta frequencies showed a similar engagement mainly localised over central and fronto-central regions. These effects were due to a stronger difference between aware and unaware trials in the natural condition, as there was a stronger power reduction for the aware than the unaware in this condition (see Figure 3b for a representative example).

The theta (4–7 Hz) and alpha (8–13 Hz) bands showed a first significant cluster mainly over occipital regions starting around 400 ms after stimulus presentation until the end of the epoch. This effect was due to a stronger visual awareness effect for the conservative criterion, as the power for aware trials in this condition was lower compared with the unaware (see Figure 3c for a representative example).

Higher frequencies such as gamma (31–80 Hz) showed small clusters mainly in a later temporal window (from around 600 ms until the end of the epoch) and interesting centro-occipital sites. Figure 3 illustrates a schematic overview of the main significant clusters (only significant F values after TFCE are shown).

To better understand the results, we computed post-hoc analysis testing the following contrasts by means of the TFCE method (p -values were also corrected through Bonferroni correction): the visual awareness effect in the conservative vs. liberal criterion, the visual awareness effect in the conservative vs. natural criterion and the visual awareness effect in the liberal vs. natural criterion.

For the conservative vs. liberal criterion, we found a significant cluster engaging at alpha and higher beta frequencies (around 30 Hz) starting around 300 ms after stimulus onset. This cluster involved also theta

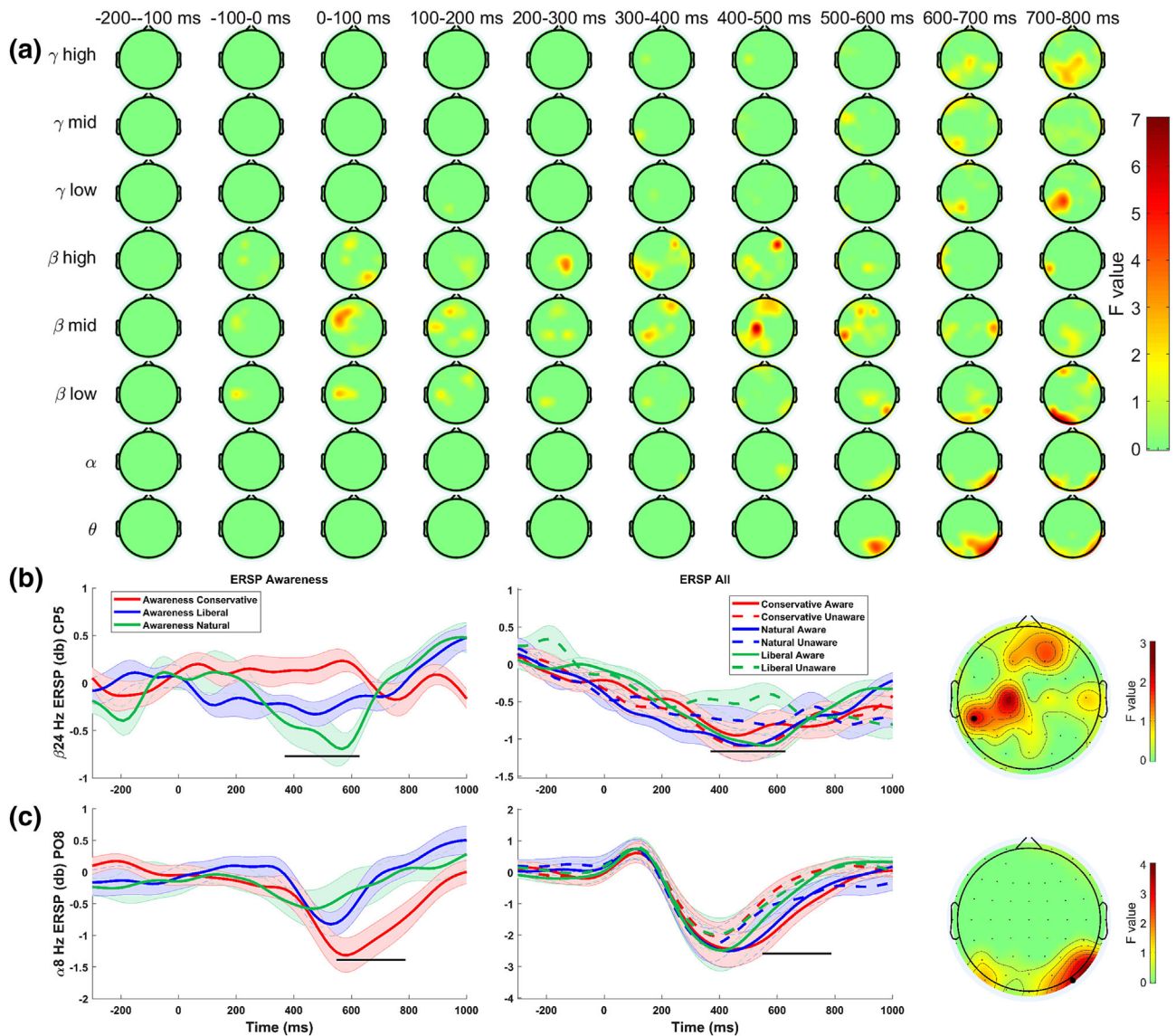


FIGURE 3 Results of interaction effects for the scalp-based time-frequency analysis. (a) Panel A shows the topoplots for the results of the interaction analysis. Each row represents the average of each frequency band (specifically, theta: 4–7 Hz, alpha: 8–13 Hz, beta1: 14–19 Hz, beta2: 20–25 Hz, beta3: 26–30 Hz, gamma1: 31–45 Hz, gamma2: 46–65 Hz and gamma3: 66–80 Hz), and each column represents the average of electroencephalography (EEG) significant clusters every 100 ms from 200 ms before stimulus presentation up to 800 ms after its onset. The topoplots show only the F values of the significant results after threshold-free cluster-enhancement (TFCE). Please note that the average on frequency bands and time bins is used only for illustrative purposes and that the analysis was conducted on each channel, frequency and time point. (b) Panel B shows the representative event-related spectral perturbation (ERSP) traces for the interaction results extracted from 24 Hz and channel 19 (CP5). On the left, the plot depicts the visual awareness effect (aware-unaware) in the three criteria (red for conservative, blue for liberal and green for natural). The black line highlights the temporal window for which the cluster was found significant. Shaded areas show the standard error. Centrally, the plot shows the traces for aware and unaware trials in all the criteria, and dashed lines represent the unaware trials. The topoplot on the right represents the average of significant results in the mid beta range (20–25 Hz) and in a temporal window between 300 and 700 ms after stimulus onset. (c) Panel C is similar to panel B but represents ERSP traces extracted from 8 Hz and channel 8 (PO8). The topoplot corresponds to the average among 8–13 Hz in a temporal window between 500 and 800 ms.

frequencies from around 500 ms. It was initially focally localised over right parieto-occipital channels, and then it gradually involved more channels over the central and posterior regions as time passed, until the end of the

epoch. This effect was mainly due to a stronger power reduction for aware trials as compared with the unaware, especially evident in the conservative criterion (see Figure 4 for representative results).

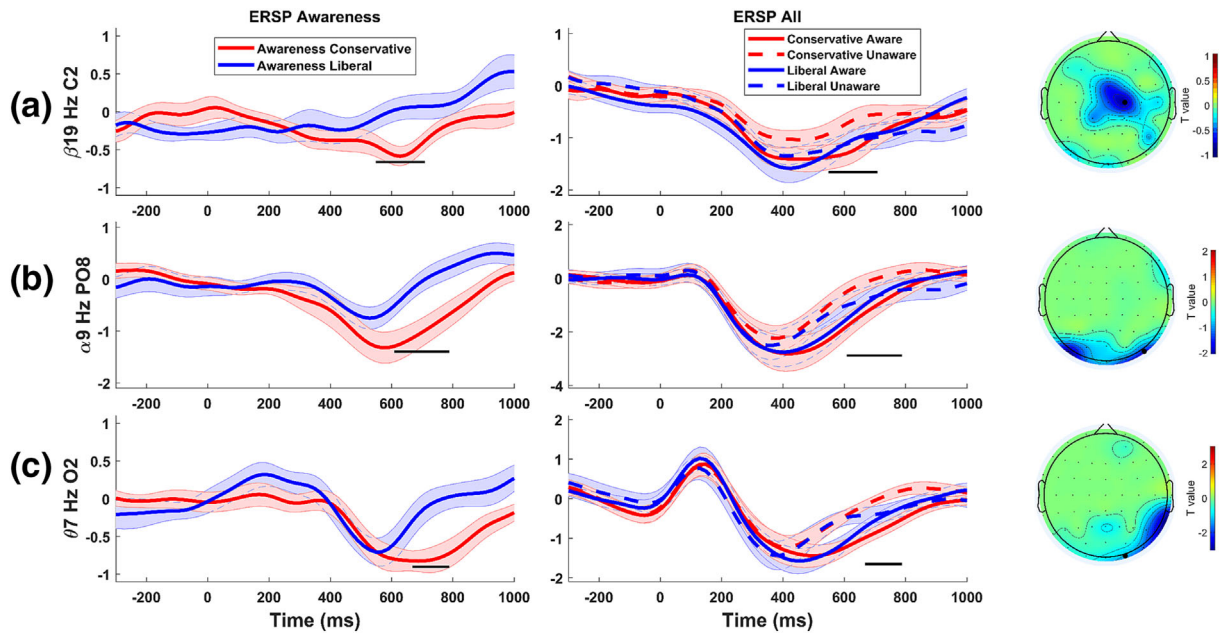


FIGURE 4 Representative results of post hoc analysis for conservative vs. liberal criteria. Each panel shows the following plots: the first one represents event-related spectral perturbation (ERSP) traces for the awareness effect (aware and unaware), followed by ERSP traces for all conditions (aware and unaware) and by the topoplot on the extreme right. Blue lines are for the liberal criterion, and red lines are for the conservative one. The dashed lines represent unaware trials for each criterion and the black line marks where the channel was found significant in time. Shaded areas show the standard error. Specifically, (a) panel A represents the results extracted from 19 Hz and channel 32 (C2), and the topoplot represents the average among 14–19 Hz in a temporal window between 600 and 900 ms. (b) Panel B represents ERSP from 9 Hz and channel 8 (PO8), whereas the topoplot shows the average between 8–13 Hz in a temporal window of 600–900 ms. (c) Panel C represents an ERSP of 7 Hz at channel 3 (O2) and the topoplot depicts the average between 4–7 Hz and 600–800 ms.

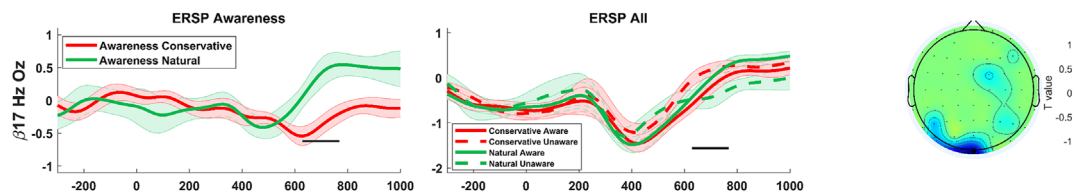


FIGURE 5 Representative results of post hoc analysis for conservative vs. natural criteria. The plot shows event-related spectral perturbation (ERSP) traces for 17 Hz at channel 2 (Oz). On the left, there is the awareness effect (aware and unaware), followed by ERSP traces for all conditions (aware and unaware). Green lines are for the natural criterion, and red lines are for the conservative one. The dashed lines represent unaware trials for each criterion and the black line marks where the channel was found significant in time. Shaded areas show the standard error. On the extreme right, the topoplot represents the average amount of 14–19 Hz and in a temporal window from 600 to 800 ms.

For conservative vs. natural contrast, the pattern showed significant clusters mainly localised in later temporal windows (from around 600 ms after stimulus presentation until the end of the epoch). This cluster mainly involved low- and mid-beta frequencies and interested channels over posterior sites. This effect was due to an opposite trend in the visual awareness effect between the two criteria (see Figure 5 for an example).

Finally, for the liberal vs. natural contrast, results showed no significant effect.

6 | DISCUSSION

The aim of the present study was to shed light on the contribution of different frequency bands on visual awareness and investigate if and how they are modulated by distinct response criteria.

Indeed, we induced different response criteria by means of task instructions in order to evaluate how visual awareness interacts with decision processing. In this way, it is possible to disentangle neurophysiological markers

associated with conscious perception from those that are modulated by post-sensory processes.

Concerning the electrophysiological results, no significant effect was found for the response criterion manipulation. This result is in contrast with a previous time-frequency study from Kloosterman et al. (2019), which found different neurophysiological markers for liberal and conservative criteria. However, it is noteworthy to say that the authors used a different approach to influence decision criterion by means of reward and penalty. It is possible that the use of stimulus-response reward contingencies is reflected in more evident differences across the two criteria as compared with the simple verbal instructions used in the present paradigm, which also led to the exclusion of many participants for not adequately shifting their response criterion. Future studies should investigate these aspects more in depth.

6.1 | Prerequisites for conscious perception

As concerns the awareness manipulation, we found the contribution of different frequency bands in the pre-stimulus period. It is likely that at this stage processes related to prerequisites of awareness take place.

First of all, we found involvement of theta frequency over mid-frontal regions, showing a main power suppression for the aware trials. Theta frequencies have been associated with cognitive control exertion (Cavanagh & Frank, 2014) and with attentional processes over the dorso-fronto-parietal network (Fellrath et al., 2016; Yordanova et al., 2017). Similarly, our results can be in line with this evidence, and the theta frequencies in this study may represent a marker of the engagement of attentional processes needed to discriminate the stimulus.

Our results on alpha frequencies are in line with previous studies showing a decrease in alpha power for aware trials in the pre-stimulus window. Indeed, this finding has been previously suggested to represent a possible neurophysiological marker of increased cortical excitability, which can lead to higher subjective awareness (Benwell et al., 2017, 2022; Mathewson et al., 2011; Samaha et al., 2017). This result is in line with the baseline sensitivity excitation model (BSEM; Samaha et al., 2020), which suggests that the baseline activation of the alpha band modulates perception directly, independently of accuracy.

Interestingly, pre-stimulus beta results resemble those found in the alpha band. Beta suppression has been previously mentioned to have a similar pattern and function to the alpha band (Benwell et al., 2022). Other previous

studies on attention have demonstrated the involvement of beta synchronisation in the integration of visual information and visual attention (Gross et al., 2004; Volberg & Greenlee, 2014; Yordanova et al., 2017). Moreover, the beta has also been suggested to be involved in the maintenance of the 'status quo', where changes in this state would lead to modulation of this frequency band (Engel & Fries, 2010). In our study, beta suppression may represent a variation of the 'status quo' to allow the elaboration of the stimulus.

In the present study, we did not find a prominent involvement of gamma frequencies, contrary to what other studies reported (Aru & Bachmann, 2009; Fisch et al., 2009; Lachaux et al., 2005). We found a stronger power suppression for aware trials in low gamma frequencies that resembled the pattern seen in beta bands. This cluster mainly involved 31–33 Hz, so it is possible that it constituted the same physiological activation as the one in the beta band, due to the overlap between high beta and low gamma. However, we found a small cluster in a higher gamma band showing higher power for aware trials and, interestingly, mainly at central regions in a temporal window until the presentation of the stimulus. Previous evidence suggested that pre-stimulus gamma can be involved in decision bias in the lateral occipital cortex (Wyart & Tallon-Baudry, 2009).

Overall, findings relative to the pre-stimulus time window need to be interpreted with some caution given the full-epoch baseline correction used, which can potentially overestimate or bias the effects occurring before the stimulus onset (but see Cohen, 2014 and Grandchamp & Delorme, 2011 as references for the methods used here). More research is thus recommended to overcome this limitation due to some methodological constraints in the task design and confirm the above conclusions.

6.2 | Correlates of visual awareness and post-perceptual processes

Concerning the results of the awareness effect in the post-stimulus window, we found an involvement of the theta band showing the same pattern over the frontal, central and posterior regions, with a stronger power suppression for aware trials as compared with the unaware trials. As previously mentioned, theta frequencies have been considered a signal of the exertion of cognitive control (Cavanagh & Frank, 2014), usually reporting higher power for the most cognitively demanding condition. In our study, it is possible that the unaware trials are those requiring more cognitive resources, in line with our behavioural results (especially for the liberal and natural criteria). Indeed, it is possible that participants in the liberal

and natural criteria were more inclined to respond that they had seen the stimulus, even when they were uncertain. This does not happen in the conservative criterion, where there is no difference between aware and unaware trials. This can be due to the fact that, in this criterion, participants were encouraged to respond that they had seen the stimulus only if they were sure. Given that the engagement of the theta frequencies was more prominent from about 400 ms after stimulus presentation, this can reflect a correlation of post-perceptual processes involving higher-order cognitive functions.

In the post-stimulus period, alpha frequencies engaged more regions over the scalp, spanning a temporal window from stimulus presentation until 700–800 ms after its onset. Studies investigating NCC with ERP analysis often suggested the VAN component as a proper correlate of visual awareness (Koivisto & Grassini, 2016; Mazzi et al., 2020; Wilenius-Emet et al., 2004). This ERP component occurs around 200 ms after stimulus presentation and is localised over occipito-temporal sites. In our ERSP study, the alpha band around 200 ms after stimulus presentation may represent a candidate for the proper correlate of visual awareness, as the topography resembles the one reported in previous ERP studies. We suggest that alpha works as a trigger for visual awareness, boosting the processing of relevant stimuli. Other previous time-frequency studies suggested an association between the alpha band and visual awareness (Mathewson et al., 2011; Samaha et al., 2020). Moreover, alpha has also been suggested to represent a general mechanism of engagement and disengagement (Jensen & Mazaheri, 2010), therefore leading to the facilitation or suppression of stimuli (Haegens et al., 2012). Alpha in later temporal windows can be involved in more post-perceptual processes, such as reactive processing to provide goal-directed behaviour (Geng, 2014), possibly being involved in the accumulation of evidence towards a decision.

Our results in low and mid-beta frequencies resembled those obtained for the alpha band, whereas those in higher beta showed a similar pattern but were especially localised over more central regions. Recent findings have already suggested that the neurophysiological function of the beta band goes beyond motor control. Indeed, the beta has been reported to be modulated by expectations (van Ede et al., 2014), working memory and decision-making (Haegens et al., 2011; Spitzer & Haegens, 2017). One possibility is that alpha and beta activity may reflect a similar mechanism, being involved in visual perception awareness and post-perceptual processes, as well as previous evidence found a similar pattern of results for these bands (e.g., Benwell et al., 2022).

For the sake of clarity, we decided to discuss the results of the post-hoc analysis to explain interaction effects. The results revealed that there was no difference between liberal and natural conditions, as also highlighted by behavioural data. This could be ascribed to the difficulty of significantly shifting their natural criterion towards a more liberal setting as participants were forced to make their decision under uncertainty. On the contrary, participants were more effective when they shifted their criterion towards a conservative setting by strictly basing their decision on sensory evidence accumulation.

The contrast between conservative and liberal criteria revealed a main involvement of theta, alpha and especially low beta in the post-stimulus period (from 300 ms) due to a stronger visual awareness effect in the conservative criterion. As previously mentioned, theta frequencies may be involved in the exertion of cognitive control, which is necessary to adopt the criterion given through the task instructions. Alpha and beta frequencies may be engaged in the selection of the relevant information and decision-making processes to provide the correct answer.

The contrast between conservative and natural criteria was mainly characterised by the main involvement of beta in later temporal windows (600 ms), possibly involving processes related to the decision. The findings in these late temporal windows may correspond only to post-perceptual processes, helping to disentangle the proper correlation of the NCC. The pattern of results resembled the one found in the behavioural analysis, where only the conservative vs. liberal and conservative vs. natural contrasts showed significant differences.

7 | CONCLUSIONS

To sum up, the present results add to a growing body of evidence suggesting that different ERSP features orchestrate together the process of visual awareness. We suggest that our findings in the pre-stimulus time window may represent markers of the prerequisite of visual awareness, whereas our post-stimulus results may reflect a mixture of the proper correlate of visual awareness and post-perceptual processes. Contrastive analysis together with the manipulation of decision bias (e.g., different response criteria) may help to disentangle the two. In our study, alpha and beta bands seem to represent good candidates for proper NCC, given their timing and topography. This study opens up a new perspective in the study of visual awareness, suggesting that more frequencies can be involved in the process and should be further investigated.

AUTHOR CONTRIBUTIONS

Alessandra Tafuro: Data curation; formal analysis; validation; visualization; writing—original draft; writing—review and editing. **Chiara Mazzi:** Conceptualization; data curation; formal analysis; investigation; methodology; validation; visualization; writing—original draft; writing—review and editing. **Silvia Savazzi:** Conceptualization; funding acquisition; investigation; methodology; project administration; supervision; validation; writing—original draft; writing—review and editing.

ACKNOWLEDGEMENTS

This research was partially supported by MIUR PRIN, grant no. 2017TBA4KS_002 and by Fondazione Cassa di Risparmio di Verona Vicenza Belluno e Ancona ‘Ricerca scientifica d’eccellenza 2018’, grant no. 2018.0861. Open Access Funding provided by Università degli Studi di Verona within the CRUI-CARE Agreement.

CONFLICT OF INTERESTS STATEMENT

The authors have no conflicts of interest to declare.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in OSF at <https://doi.org/10.17605/OSF.IO/A39TH>.

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PEER REVIEW

The peer review history for this article is available at <https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ejn.15988>.

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How to cite this article: Tafuro, A., Mazzi, C., & Savazzi, S. (2023). The spectral dynamics of visual awareness: An interplay of different frequencies? *European Journal of Neuroscience*, 57(12), 2136–2148. <https://doi.org/10.1111/ejn.15988>