

## **Anticipation shapes conscious perception**

Despite the inherent difficulty of studying private phenomena, neuroscience has made significant progress. Nonetheless, it is still unknown to what degree the frontal lobes play in forming our subjective experiences of the world. Some contend that our ability to predict future events shape our conscious experiences: mounting behavioural and neural findings corroborate this view. However, little work has investigated how temporal expectation –i.e. phasic alertness—can modulate the neural correlates of consciousness. The present study investigates this lacuna using a target discrimination task; we combined temporal cueing with backward masking and simultaneous recordings of electroencephalography (EEG). For only half of the trials, participants were cued to expect when the forthcoming target would onset. On every trial, participants provided both type I responses (discrimination of the target) and type II responses (subjective report). Our behavioural results show that temporal cueing boosts perceptual sensitivity, perceptual awareness, and ideomotor processing. At the neural level, we show that cueing is associated to a greater amplitude of the P300/LP and a smaller amplitude of the VAN, two correlates of consciousness. Moreover, cueing was associated to increased power in frontal and posterior theta oscillations, as well as a decrease in frontal and posterior alpha and low beta oscillations, likely indexing preparation. Together, these results elucidate the role of temporal predictions in perception, illustrate a boost in the neural markers of consciousness, and underline the importance of predictions and the frontal lobes in our conscious experiences.

### **1.0 Introduction**

Our lives are embedded in rich conscious experiences: from the vibrant sounds of music, to the details of a quaint scene. Notwithstanding, the scientific investigation of subjective experiences remains challenging because consciousness is a fundamentally private phenomena (Koch et al., 2016; Seth, 2010). To overcome these obstacles, scientist have developed an array of methodologies and analytical tools which gave way to several advances in the field: identifying many potential neural markers of conscious processing, among which we distinguish gamma activity in the sensory cortex and the P3b Event Related Potential (ERP) (Koch et al. 2016; Dehaene & Changeux, 2011). Despite these advances, many still debate the role of high-order processes in conscious perception. Some contend that higher order processes shape our understanding of the world (Lau & Rosenthal, 2011; Dehaene & Changeux, 2011). While others argue that the frontal lobes minimally contribute to our subjective experiences (Frässle et al., 2014; Malach, 2011). The current study wishes to tackle these questions, asking how anticipation shapes our conscious experiences and what are the underlying mechanisms at play.

To begin, researchers have identified potential candidates for neural correlates of consciousness which divided the field amongst their proponents. For example, some propose late ERP markers of consciousness such as the P300 and the LP in line with global-workspace theory (Dehaene & Changeux, 2011). While others highlight earlier ERP components like the Visual Awareness Negativity *VAN* (Rutiku et al., 2015; Koivisto & Revonsuo, 2010; Eklund & Wiens, 2018). In line with this, some argue for the *VAN* as an index of recurrent local processing in the posterior visual areas, relating to phenomenological experience while also contending that the P300/LP reflects global recurrent processing in the parietal hubs, reflecting access of conscious information (Andersen et al., 2016; Koch, Massimini, Boly, & Tononi, 2016). Despite the extensive research on these markers of consciousness, few have investigated how temporal predictions shape these correlates of consciousness

While several theories of consciousness highlight the central role high-order cognitions play in conscious perception, their interpretation has sparked debate (Lau & Rosenthal, 2011). One study demonstrates that predictions induce frontal activity in the vMFC (Summerfield et al., 2006). Moreover, work on auditory perceptron shows that anticipation of upcoming events

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engages the motor cortices (Morillon, & Baillet, 2017). Others contend that all these results can be interpreted with an opposing theory of consciousness in mind whereby the frontal lobes play a minimal role (Malach, 2007; Malach, 2011; Zeki, 2008). Likewise, some experimental work argues that the frontal brain primarily plays a role in introspection, rather than perception itself (Frässle et al., 2014). Taken together, this work illustrates a complex picture, whereby the frontal lobes may play a role in consciousness beyond access and introspection.

The role of anticipation in consciousness also remains unclear. Anticipation forms one of the central capacities of the frontal-lobes. Research utilising temporal cueing consistently shows benefits across motor processing; improvement in perceptual processing is less clear (Vangkilde et al., 2012; Correa et al., 2006; Martens & Johnson, 2005). Samaha & Postle have argued that the phase of alpha in the occipital lobes reflects temporal resolution of conscious perception, which if biased by cueing will improve conscious processing (Samaha & Postle 2015; Samaha et al., 2015). A nuanced picture using signal-detection theory is needed to better understand if and how anticipation can improve target processing.

The current project aims to address these questions using an EEG within-subject design; we manipulate temporal expectations on a trial by trial basis by cueing participants to the onset of forthcoming target. Participants will subsequently discriminate the target and provide a subjective report. Our analysis will focus on linking the behavioural benefits observed by temporal cueing (i.e. alertness) to the proposed neural markers of consciousness and isolate the neural underpinnings of temporal cueing. We hypothesize that temporal cueing will not only improve motor performance, but will also improve participants' perceptual sensitivity, and subjective reports. In terms of the neural results, we hypothesize that cueing will induce a greater amplitude of the neural correlates of consciousness (i.e. the VAN and P300). Cueing should also reflect a change in spectral power across the alpha band and a gain in motor preparation (beta). Frontal markers of cueing should bias conscious processing. Lastly, in accordance with theories of consciousness, cueing should bias functional connectivity—reflecting an interaction between subjective report and condition. Together these results will elucidate a mechanism of conscious perception whereby frontal anticipation will lower the threshold of conscious perception.

## **2.0 Methods**

### **2.1 Participants**

We recruited 30 individuals (19 female, 21.333 years old  $\pm$  2.279) from the McGill University to participate in our study. All subjects had corrected-to-normal-vision and no neurological or psychiatric conditions. Participants provided written informed-consent before the experiment.

### **2.2 Apparatus, Stimuli, & Procedure**

Target stimuli were presented on an LCD screen at a viewing distance of 60 cm in a dimly lit room. Stimuli were generated and presented using the psychtoolbox toolbox running in MATLAB 2015b (MathWorks, Natick, MA). Each subject completed a practice session of 50 trials and 1200 trials of a forced two-choice target discrimination task. Each trial began with a central fixation point for participants to maintain their gaze. The duration between the fixation and target (SOA) was jittered between 1001 ms and 2052 ms, and thus the fixation conveyed no temporal expectations. On half of the trials, the fixation point would then flash indicating to the participants the forthcoming onset of the target (720 ms). On the other half of trials, no cue was presented and thus, participants had no expectations (see Figure 1). The target, a Gabor patch, was presented for 26 ms before being removed and quickly masked at two mask latencies (26 and 52 ms). Participants made their first response: discrimination of the target orientation. Afterwards, the screen would prompt participants to indicate their subjective experience of the

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target (i.e. *SEEN or NOT SEEN*). Participants were encouraged to answer both quickly and accurately, not sacrificing one for another. Subjective reports were operationalized for all participants as *any* subjective experience of the target. The inter-trial period was 1001ms. Trials were split into 10 equally size blocks. Participants were encouraged to take small break during these blocks and were offered water to remain alert. The total duration of the experiment, including EEG preparation and the psychophysics task, was approximately 2.5 hours long.

### 2.3 Behavioural Measures

Participants' accuracy, discrimination reaction times (RTs), and subjective reports (i.e. whether they reported seeing the target) were collected for each trial. Data were modeled accordingly using three strategies: for Type 1 responses (discrimination) RTs were modeled using ex-gaussian parameters, Type 1 accuracy were modeled with signal detection theory, and subjective reports were modeled using linear regressions. The ex-Gaussian function convolves the normal distribution with an exponential component to account for the skewed nature of reaction times, returning three parameters: Mu, Sigma, and the Tau exponential component (Heathcote, Popiel, & Mewhort, 1996). Data were fit using the R package (retime). Signal Detection theory allows one to decompose accuracy to two parameters: one's sensitivity to a signal, and their criterion for report (Macmillan & Creelman, 2005). We calculated perceptual sensitivity  $d'$  and decision criterion C in the following manners:

$$d' = z(\text{hit rate}) - z(\text{false alarm})$$
$$C = -0.5 * (z(\text{hit rate}) + z(\text{false alarm}))$$

This model will allow us to capture nuanced changes accounting for any bias in reports participants may have. Lastly, we modeled subjective reports using linear regression.

### 2.4 EEG Acquisition and Preprocessing

EEG was collected from 64 Ag/AgCl active gel-based electrodes (Brain Products GmbH) and 2 bipolar external electrode pairs placed around the eyes to monitor eye movements and blinks. All impedances were kept below 10 kΩ. Data was collected online at 1000Hz, without any filters. Data was preprocessed using both brain vision analyzer 2 (Brain Products GmbH,) and brainstorm (Tadel et al. 2011). First, data was high-passed filtered at 0.1 Hz, down sampled to 250 Hz, and noisy channels were interpolated. EEG data was re-referenced to an average reference. Bad segments were then marked, and ICA was used to remove ocular artifacts from the data. Data were then exported into brainstorm where timestamps were corrected with regards to a photodiode—collected simultaneously with the recording. Before continuing, the data analysis was split into two branches: ERPs and spectral/functional connectivity. This was done as ERPs typically low-pass filter their data (30 Hz), prior to segmenting it; whereas, for our other set of analysis no low-pass filtering was required.

### 2.5 ERP analysis

Data was segmented into epochs from -200 to 1000ms after target onset. ERPs were extracted in brainstorm: VAN and P300, components were averaged across 4 conditions—cued vs not cued across seen vs not seen. The VAN and P300 are components associated to visual awareness and emerge after contrasting (subtracting) the average waveforms of trials where the participants reported seeing the target from trials where the participant reported not seeing the target. This was done separately for each cueing condition. Once the time-series for all four conditions were extracted, PLS analysis was preformed to determine which timepoints and

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electrodes conveyed meaningful associations to the task conditions (see section 2.9). Subsequently, custom MATLAB scripts preformed a serial pairwise permutation t-test across all time points on the previously identified electrodes from the PLS analysis to determine where the two conditions (cued vs not cued) differed statistically from one another using the averaged difference waves obtained per participant. To control for false positives, a permutation approach (10,000 permutations) was taken such that at each timepoint a null distribution was created by scrambling the association between cued and not cued trials and the true t-value was compared to this distribution (significance was determined at  $t > 95\%$  percentile of the null distribution) (see Maris & Oostenveld, 2007 for details).

### **2.6 Spectral analysis**

Time-frequency plots were extracted using brainstorm. Epoched data was transformed at each channel and trial by convolving the timeseries with a family of complex Morlet wavelets spanning 1–50 Hz in 1-Hz steps with a mother wavelet of a temporal resolution of 3 seconds (FWHM) at a central frequency of 1 Hz. The absolute value of the resulting complex number is squared to obtain power. This was done separately for trials where participants were cued and not cued; averages of the resulting time-frequency plots for each condition can be seen in Figure (4.a). PLS analysis was conducted to determine which patterns of oscillations covary with cueing (see section 2.9). From the PLS results, three bundles of electrodes were selected based on visual inspection: a frontal cluster, a parietal/central cluster, and a posterior cluster (see Supplementary info). A single time-frequency plot was obtained per bundle by averaging the time frequency plots within participants across the electrodes constituting the bundle.

### **2.7 Functional Connectivity**

Functional connectivity was computed using Amplitude Envelope Correlation (AEC) in brainstorm. This method is particularly useful for FC in EEG as it has been shown to be both reliable and valid (replicating resting state networks observed in fMRI) (Colclough et al., 2016; Brookes et al., 2011; Hunt et al., 2016). To compute AEC, we first filter the timeseries data into one of five defined frequency bands: 1) delta  $\delta$  (1–4 Hz); 2) theta  $\theta$  (4–8 Hz); 3) alpha  $\alpha$  (8–13 Hz); and 4) beta  $\beta$  (13–30 Hz) 5) gamma  $\gamma$  (30–50Hz). Amplitude envelopes were generated via the Hilbert transform for each sensor and participant, across 3 second windows. Pearson correlations were then computed between all sensor pairs for the subsequent amplitude envelopes. This generated a 64x64 correlation matrix for each 3 second window, across all subjects and recording sessions. An average AEC matrix was generated for each subject, at each frequency band, and across the four conditions.

### **2.8 Regression Models**

Inferential statistics were done by fitting hierarchical regression models (Gelman & Hill, 2006), as implemented by the lme4 package (Bates, Maechler, Bolker, & Walker, 2015), in R Studio (RStudio-Team, 2016). Goodness-of-fit of the models was evaluated in a step-wise fashion using chi-square tests, models that significantly reduced the Bayesian Criterion Information (BIC) were chosen. For a complete summary of the models fit, please see the tables in the supplementary info. Linear models were applied to d prime, criterion; and reaction time estimates of mu, sigma and tau; logistic regressions were applied to subjective reports (seen vs not seen) and accuracy.

### **2.9 PLS Analysis**

Partial Least Squares (PLS) offers researchers a set of multivariate analysis techniques to relate two matrices of data to one another—a fundamentally useful technique in neuroimaging

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and electrophysiology where multiple comparisons and few observations are problems (McIntosh & Misic, 2013; Misic et al., 2016). The goal of PLS is to describe the two matrices ‘X’ (neural data) & ‘Y’ (behavioural data or design matrix) in terms of a linear combinations of variables which maximally covary with one another, relying on singular value decomposition. To assess the statistical significance of the latent variables, permutation testing is employed; whereas, bootstrapping is done to evaluate the reliability of individual weights obtaining a bootstrap ratio which can be interpreted as a z-score—which features of the neural data reliably contribute to the contrast values (Efron & Tibshirani, 1986).

Our PLS analysis will rest on three types of neural data, ERP time series, time-frequency spectral power, and functional connectivity as described in sections 2.5-2.7. The behavioural matrix will ultimately reflect a 2x2 design whereby we cross cueing with the subjects’ subjective reports for both ERP time-series and functional connectivity. Whereas, the behavioural matrix for time-frequency power will only contrast cued from not cued trials. PLS analysis was conducted in MATLAB 2018a (MathWorks, Natick, MA) using the toolbox provided by Rotman-Baycrest and following the methods employed in (McIntosh & Lobaugh, 2004). For the ERP time series, PLS was ran over 19264 features for 10,000 permutations and bootstraps, over 3203200 features and 1000 permutations/ bootstraps for time-frequency power, and over 2080 features and 10,000 permutations/ bootstraps for functional connectivity.

## 3.0 Results

### 3.1 Behavioural Results

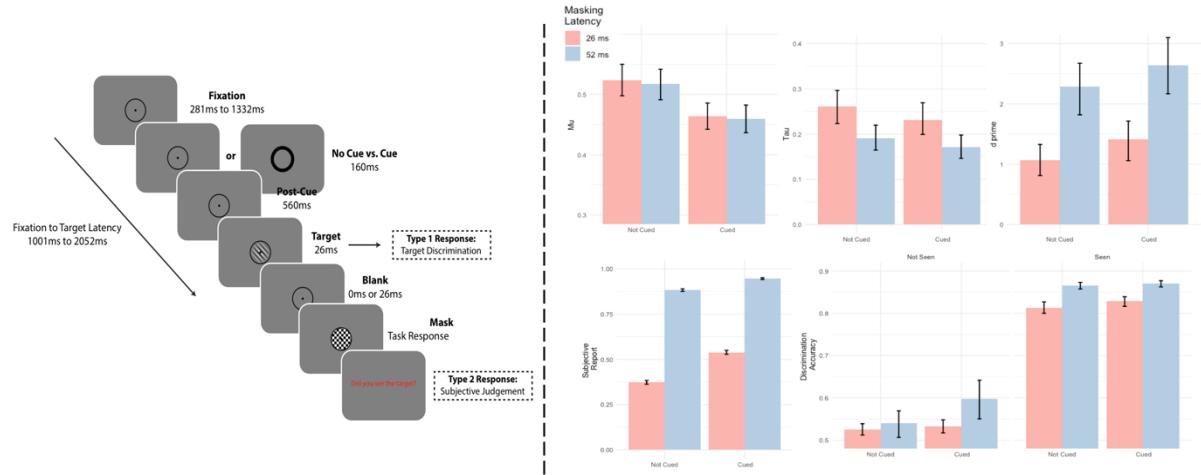
#### 3.1.1 Type I Response: ex-Gaussian parameters and Signal Detection theory

Ex-Gaussian parameters were evaluated using hierarchical linear regression models with cueing and mask latency as fixed factors and subjects as a random factor. Models were built in a step-wise fashion for mu, sigma, and tau parameter separately. The best fitting model and most parsimonious for mu included only a cueing ( $\chi^2(1) = 62.7084$ ,  $p < 0.05$ ; see Table 3). Cueing ( $\beta = -0.058918$ ,  $SE = 0.006223$ , 95% CI [-0.07117657, -0.04665850]) was a reliable predictor. While the best fitting model for tau included both masking and cueing ( $\chi^2(1) = 13.0943$ ,  $p < 0.05$ ; see Table 5), with masking ( $\beta = -0.024768$ ,  $SE = 0.007552$ , 95% CI [-0.03956079, -0.009974348]) and cueing as reliable predictors ( $\beta = -0.064742$ ,  $SE = 0.007552$ , 95% CI [-0.07953541, -0.049948969]). Similarly, the best fitting model for d prime included both cueing and masking effects ( $\chi^2(1) = 18.6549$ ,  $p < 0.05$ ; see Table 1). Both cueing ( $\beta = 0.35075$ ,  $SE = 0.07791$ , 95% CI [0.1981308, 0.5033666]) and masking ( $\beta = 1.22439$ ,  $SE = 0.07791$ , 95% CI [1.0717691, 1.3770050]) were reliable predictors of d prime. Taken together, these results emphasize that alertness boosts target processing and response selection.

#### 3.1.2 Type II: Subjective reports

We ran two sets of analysis for subjective reports: hierarchical logistic regression models as well as models with subjective report predicting accuracy. Firstly, the best fitting model for Type II included both cueing ( $\beta = 0.82973$ ,  $SE = 0.03071$ , 95% CI [0.7696418, 0.8900344]) and masking ( $\beta = 2.93984$ ,  $SE = 0.03648$ , 95% CI [2.8687193, 3.0117637]) as reliable effects ( $\chi^2(1) = 9537.5848$ ,  $p < 0.05$ ; see Table 6). The best fitting model for discrimination accuracy included three main effects of subjective report, cueing and masking ( $\chi^2(1) = 30300$ ,  $p < 0.05$ ; see Table 7). All three are reliable predictors of accuracy: subjective report ( $\beta = 1.44215$ ,  $SE = 0.03563$ , 95% CI [1.37245315, 1.5121293]), cueing ( $\beta = 0.08112$ ,  $SE = 0.02905$ , 95% CI [0.02416968, 0.1380677]), and masking ( $\beta = 0.38600$ ,  $SE = 0.03458$ , 95% CI [0.31819121, 0.4537552]). These findings emphasize that alertness improves subjective experience of the target, this cannot be explained by cueing’s effect on accuracy alone.

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**Figure 1.** Schematic of task and behavioural findings. LEFT. Overview of temporal-cueing task. RIGHT. Bar plots depicting behavioural results. Both  $d'$  prime and subjective report revealed two main effects: cueing and mask latency. Whereas, when controlling for subjective report, accuracy had three main effects: cueing, mask latency, and subjective report. Main effect of cueing over reaction time ex-gaussian parameters.

### 3.2 ERP Results

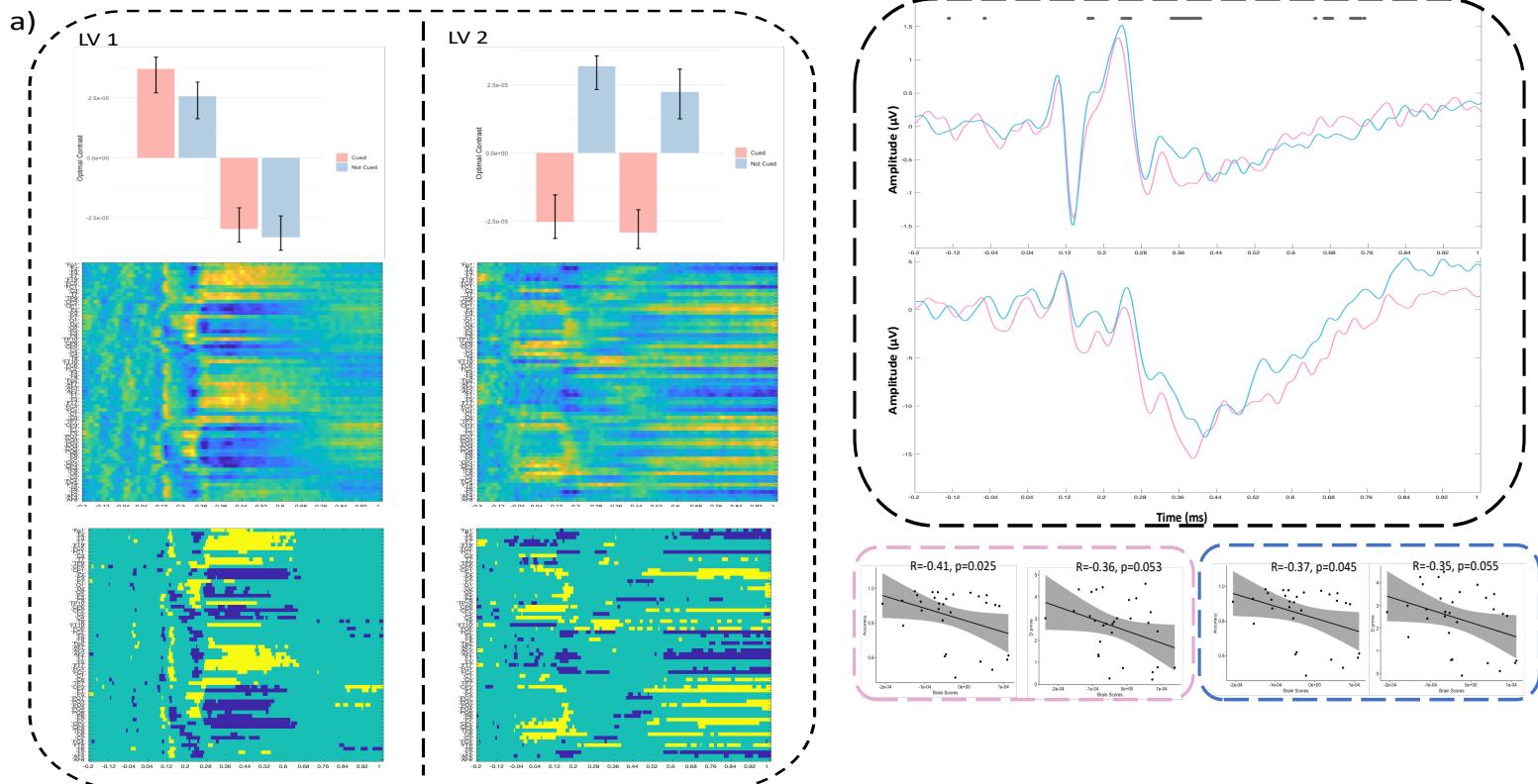
PLS analysis, as depicted in Figure 2, indicated that two latent variables were significant: LV1 differentiating between seen and not seen trials ( $p < 0.0005$  and 54.67% covariance accounted for) and LV2 differentiating between cued and not cued trials ( $p < 0.0005$  and 40.84% covariance accounted for). In the case of LV1 positive bootstrap ratios are associated to greater amplitude (negative potential) in the not seen condition, whereas negative bootstrap ratios would be associated to less amplitude (i.e. a positive potential) in the not seen condition. One can see three key patterns emerge from the data: the ERP potential associated to the P100, the VAN and the P300/LP (fig 2a). This is made evident when we threshold the map at a bootstrap ratio at  $> \pm 2.58$  corresponding to the 99% confidence interval. This threshold was chosen to conservatively gauge the most prominent patterns of the weights. Furthermore, a hint of the CNV (Contingent Negative Variation), an ERP marker of expectation, prior to cue onset is visible as well for LV2 (fig. 2b). The CNV appears frontal-centrally and indexes one's expectation about the upcoming events—the more negative the greater the prediction (Van Rijn et al., 2011; Mento et al., 2015; Mento 2013). Plotting the ERP centered at the cue unveils the CNV (see supplementary info, Supp. Fig. 2), and thus serves as a verification of our cueing manipulation. In all, these results paint a picture of the ERP dynamics underlying subjective experiences and cueing.

A secondary set of inferential statistics were run to test whether the VAN and the P300/LP were significantly different across cueing conditions (Maris & Oostenveld, 2007). A subset of electrodes, identified from the PLS analysis, were averaged and fed into a serial permuted t-test. The permutation t-test revealed a significant difference for the VAN around 170–250ms after target onset, largest for the most posterior electrodes. Additionally, there was a significant difference for the P300/LP component, where cueing induced a more positive potential around 300–400 ms and lasting much later into ~520ms (see Fig. 3). Together these results demonstrate that temporal expectation alters the neural correlates of consciousness.

Next, we wished to identify how these shifts in the neural correlates of consciousness relate to the behavioural results. For each condition of LV1, we ran a Pearson correlation between the brain scores obtained for that condition and the subsequent accuracy. Significant relationships for the two Seen conditions (i.e. Seen Not cued and Seen cued) were obtained.

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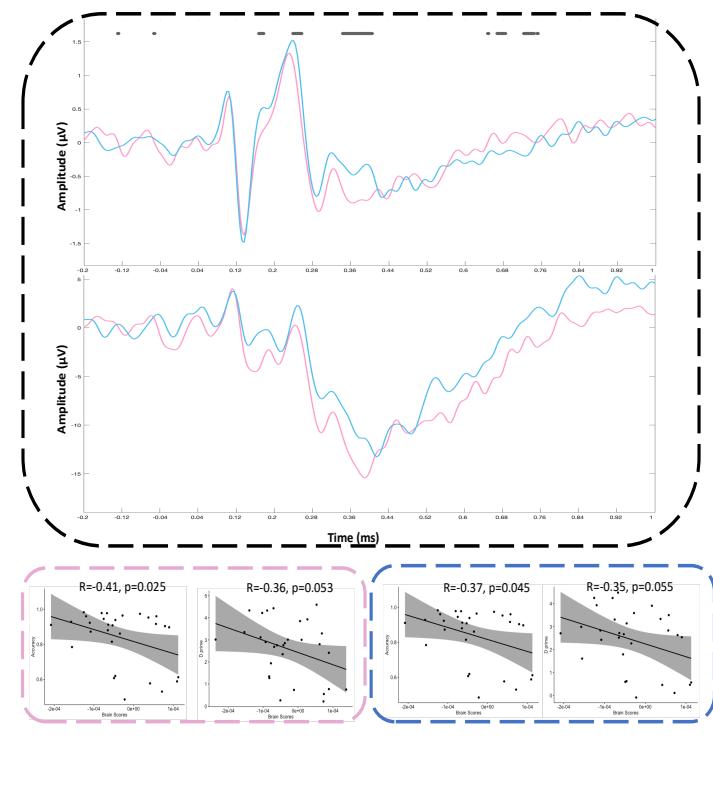
Similarly, to explore whether this reflects a change in perceptual sensitivity, we ran another set of exploratory analysis which yielded some evidence that this relationship with accuracy is driven by perceptual sensitivity (see Figure 3 and supplemental info).



**Figure 2.** Results from PLS analysis on ERP time-series. a) two latent variables were significant: LV1 contrasts Seen and Not Seen trials, bootstrap ratios are plotted blow and thresholded bootstrap ratios ( $>2.58$ ) reveals the VAN and LP component. LV2 depicts a contrast between cued and not cued trials. Bootstrap maps depict a negative component positively associated to cueing (the CNV).

### 3.3 Spectral Results

To identify spectral changes in relation to anticipation we ran a time-frequency analysis over the entire feature space (64 electrodes x 50 frequencies x 1001 timepoints). The PLS analysis revealed one significant latent variable of cueing ( $p < 0.0005$  and accounting for 99.99% of covariance). Plotting the time-frequency maps over all electrodes reveals three significant spatial clusters that maximally covary with cueing: a posterior occipital cluster, a central-parietal cluster, and finally a frontal cluster (see supplemental info). Figure 4 b-c plots the average bootstrap ratios for each of the three clusters and thresholded bootstrap maps ( $bsr > 2.58$ ). A positive bootstrap ratio would be associated to an increase in spectral power, whereas a negative bootstrap ratio would be associated to a decrease in spectral power for cueing. Cueing induced change across several oscillations: alpha, beta and theta. Changes in theta are greatest across the frontal and most posterior electrodes; both showing a sustained increase in power until target onset. Due to the nature of Morlet wavelets, poor temporal resolution at the lower frequencies



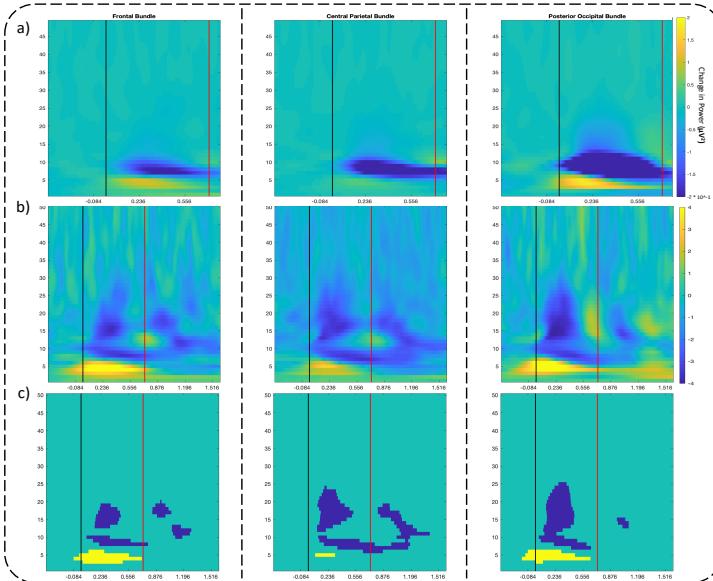
**Figure 3.** a) Difference waves for both cued (pink) and not cued (blue) trials across occipital and parietal electrodes. Grey dots mark significant differences: the VAN (top), showing a greater negative potential for not cued trials; and the P300 (bottom), depicting a greater positive potential for cued trials. b) Correlation plots of brain scores per condition with behavioural outcomes.

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caused temporal smearing. Next, we wished to associate these patterns to the behavioural results. We correlated participants' brain scores obtained from the PLS to three behavioural metrics: d prime, subjective reports, and mean RT estimated from the ex-gaussian distribution. None of the tested correlations were significant (see supplementary info). Overall, these results point to multiple neural-systems for anticipating target onset: as alpha is typically associated to attention, beta motor preparation and processing, and theta executive control.

### 3.4 Functional Connectivity Results

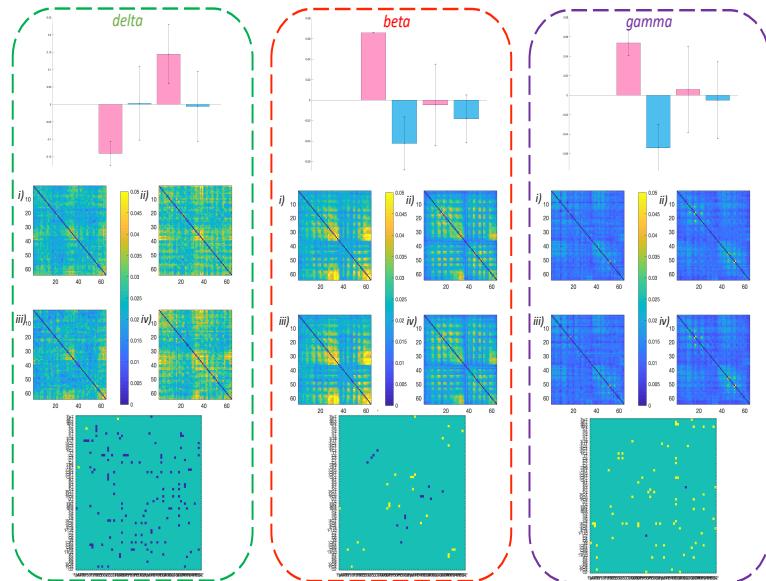
Lastly, we conducted exploratory analysis to identify changes in functional connectivity across cueing. The alpha and theta bands revealed no significant contrasts ( $p < 0.05$ ). Whereas, the beta and gamma band had one significant contrast differentiating between the two not seen conditions (beta:  $p < 0.05$  accounting for 51.09% of the variance; gamma:  $p > 0.05$  accounting for 57.33% of the variance) (see Fig. 5). The delta band also had a significant contrast differentiating between cued seen and not seen trials ( $p < 0.05$  accounting for 45.66% of the variance).



**Figure 4. PLS results for time-frequency power.** a) Baseline corrected change in spectral power due to cueing. Black line depicts the onset of the cue, whereas the red line highlights the onset of the target. b and c) Depict unthresholded and thresholded maps of the bootstrap ratios computed over three clusters of electrodes, respectively. Cue onset elicited three changes: an increase in frontal-posterior theta, a decrease in alpha power, and lastly a decrease in beta power.

## 4.0 Discussion

The present study explored how alertness and expectations shape our conscious experiences. Firstly, we show several behavioural benefits for temporal expectation: on trials where one can predict when the target will appear, participants displayed higher perceptual sensitivity, faster processing of the target, and more frequent subjective reports. We are not the first study to demonstrate these benefits. Yet, previous works have failed to demonstrate



**Figure 5. Functional connectivity.** First row depicts the contrasts plotted for all four conditions (seen vs not seen, cued vs not cued) for the three frequency bands of interest (delta, beta and gamma respectively). The second row depicts the FC matrices for the three bands across the four conditions i) not seen cued ii) not seen not cued iii) seen cued iv) seen not cued . The last row depicts the thresholded FC bootstrap ratios for the significant contrast.

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consistent results across perceptual processing (Samaha et al., 2015). Unlike previous work on temporal expectations, our current project did not titrate performance nor subjective reports and thus allowing us to track any behavioural benefits of cueing directly.

Our neural findings compliment the behavioural results and provide us with a clearer picture on how top-down cognitions shape the processing of visual information. Firstly, we show that the P300 and Late Positivity are greater in amplitude across cueing conditions. This coincides with the global workspace theory, as cueing prepares and boosts the widespread broadcasting of information and thus leads to more frequent reports of conscious experiences (Dehaene & Changeux, 2011). On the other hand, we show that the VAN is greater for not cued trials, likely reflecting more local processing and a greater forward sweep for unexpected stimuli (Andersen et al., 2016). One may interpret these findings in the framework of a “prediction error” reflecting greater processing needed for unpredicted targets. Further works needs to elaborate this topic. Despite a dense field studying ERP markers of consciousness, we are the first, to our knowledge, to specifically demonstrate the modulations of the VAN and the P300 by temporal predictions in dissociable ways.

Furthermore, we correlated brain scores obtained for the first latent variable—associated to the neural correlates of consciousness—to the behavioural results. Accuracy in each condition correlates with the brain scores. This is also suggested ( $p=0.05$ ) with our d prime (see Fig. 3). As there was no shift in criteria: all the benefits of cueing are manifested in a boost of perceptual sensitivity, and thus it is unsurprising that accuracy and d prime show similar patterns. Moreover, this relationship is only observed for the seen condition. One can speculate why this the case: perhaps participants guessed more often when they reported not seeing the target. The global workspace theory would argue that target processing failed to reach a “conscious threshold” and thus the activity simply died out (Dehaene & Changeux, 2011). In accordance with this theory, the neural patterns were too weak and thus this could explain why no association between the brain scores and behaviour are found.

Furthermore, our work highlights the neural correlates of temporal expectation. PLS analysis reveals three primary bands, after bootstrapping, had meaningful weights: theta, alpha and beta. The theta band is most prominent in the frontal lobes and the posterior electrodes over the entire duration of the cue-target SOA. Power in the theta band, primarily in the frontal lobes has been associated to executive functions and cognitive control (Albouy et al., 2017; Cavanagh & Frank, 2014). In contrast, the decrease in alpha power likely reflects sensory processing and subjective awareness (see review Jensen, & Mazaheri, 2010; VanRullen, 2016). Both theta and alpha have long been implicated in vision research and have suggested a dichotomy between visual attention (~7 Hz) and visual processing (~11Hz) (VanRullen, 2016). Our data corroborate this view. It has been theorized for several years that a decrease in alpha in the occipital lobes reflects a disinhibition of the sensory cortex, as one prepares for incoming information. More recent proposals suggest that alpha likely divides the upcoming information into bit-sized 100ms chunks for later processing (VanRullen, 2016). Taken together, we can theorize that the frontal lobes induce this change in alpha through modulations of visual attention (theta). And lastly, the observed change in beta power likely reflects motor preparation (Tzagarakis et al., 2015; Morillon, & Baillet, 2017). As we observe several behavioural gains across RTs, perceptual sensitivity, and subjective reports, it is unsurprising that we find many neural correlates of preparation. The brain is unlikely to take a single path to ready itself for upcoming information. This is reflected in the correlation to the brain scores for the spectral results: none of these associations were significant. These changes in spectral patterns unveil at least three different mechanisms and thus do not reflect a single measure of behavioural performance.

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Changes in FC were observed across cueing and subjective reports. This work was exploratory. Bootstrap ratios reveal islands of changes across the three bands, yet there are no clear patterns emerging in any specific network. One could speculate, however, that the change in beta connectivity is a reflection of motor preparation, whereas gamma would index visual processing. The delta band is also difficult to draw any strong conclusions as this band is difficult to measure with scalp electrodes as it is susceptible to artifacts like blinks, and slow drifts induced by sweat. These preliminary results serve as the foundation for further exploration with spatially accurate and robust measures of FC.

While the present study addresses questions about the neural mechanisms of alertness and conscious perception, several limitations hinder interpretations. Firstly, the ERP results were collapsed across masking condition. Moreover, because we did not titrate subjective reports some cells have few trials: relative blindsight approach could address this (Lau & Passingham, 2006). Neural data rested on trial averaging to reduce noise, whereas a growing technique in the literature has focused on single trial regressions to associate neural patterns to behavioural measures (Samaha, Lemi, & Postle, 2017). This approach proves to be more sensitive to relate behaviour to EEG. Lastly, the relationship between the neural results and the behavioural findings in the current paper requires further clarification.

Despite these challenges, we demonstrate how the frontal brain, and more specifically temporal expectations, shape conscious experiences. EEG offers a unique peephole into how the brain processes information with impressive temporal resolution. Understanding what these neural markers probe is at the heart of much ongoing research in the field. In this regard, our work corroborates the view that conscious experiences are built from the influence of top-down factors influencing bottom-up signals. Our internal models of the world not only shape how we interact with it, but also how we experience it.

Future work could titrate subjective reports across cueing conditions which would allow us to paint a better picture of which neural responses relate to the subsequent behavioural benefits observed. Addressing how metacognition (i.e. confidence) plays a role in alertness is also, for the most part, an unanswered question. Moreover, some recent work on phase (Samaha et al., 2015) has suggested biasing the phase of alpha as a key path the frontal brain may take to predict upcoming events. In line with this work, phase-amplitude-coupling (PAC) seems a likely oscillatory marker to explore for a fine-grained reflection on the dynamics at play.

## **5.0 Conclusion**

The present work as a whole demonstrates how predictions and the frontal lobes mould our conscious experiences. We demonstrate that temporal predictions of the forthcoming target boosts, not only, ideomotor processes, but also improves perceptual sensitivity, and increases reports of visual awareness. This translates to a modulation in the neural correlates of consciousness: we observe a greater amplitude of the P300/LP, while also a decrease in the VAN. ERP markers of cueing also confirm our manipulation (i.e. the CNV). Spectral markers of cueing indicate a decrease in alpha both posteriorly and frontally, a decrease in beta power, and an increase in frontal theta. Each band has previously been associated to perceptual preparation and visual attention, motor preparation, and top-down control respectively. Taken together, these results confirm the perceptual and motor benefits of temporal expectations on behaviour, highlight the importance of the frontal lobes in anticipation, depict how predictions alter the neural correlates of consciousness, and exemplify the many ways the brain can predict.

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