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Authors: Luca Tarasi, Giuseppe di Pellegrino, Vincenzo Romei

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Are you an empiricist or a believer? Neural signatures of predictive strategies in humans

Luca Tarasi ^a, Giuseppe di Pellegrino ^a, Vincenzo Romei ^{a,b}

^a Centro Studi e Ricerche in Neuroscienze Cognitive, Dipartimento di Psicologia, Alma Mater Studiorum – Università di Bologna, Campus di Cesena, via Rasi e Spinelli, 176, 47521 Cesena, Italy

^b IRCCS Fondazione Santa Lucia, Via Ardeatina, 306, 00179 Rome, Italy

Corresponding Author:

Vincenzo Romei,

Centro Studi e Ricerche in Neuroscienze Cognitive,

Dipartimento di Psicologia, Alma Mater Studiorum – Università di Bologna, Campus di Cesena, via Rasi e Spinelli, 176. 47521 Cesena, Italy.

E-mail: vincenzo.romei@unibo.it

Abstract

Predictive coding theory suggests that prior knowledge assists human behavior, from simple perceptual formation to complex decision-making processes. Here, we manipulate prior knowledge by inducing uninformative vs informative (low and high) target probability expectation in a perceptual decision-making task while simultaneously recording EEG. We found that priors did not impact sensitivity (d') but did shape response criterion (c), being more liberal for high expected trials and more conservative for low expected trials. Importantly, we mapped the neural signature of this criterion shift, with liberal and conservative trials characterized by low and high posterior alpha amplitude, respectively. Moreover, we demonstrated that inter-areas communication along the fronto-parietal-occipital pathway is linked to the strategic tuning of sensory areas. Specifically, whereas parieto-occipital alpha synchronization facilitates the exploitation of expectancy-type information by shaping pre-stimulus alpha amplitude in a prior-dependent fashion, fronto-parietal theta coupling mediates a supervisory process on the predictive machinery, attenuating the impact of prior on sensory processing. These findings aided us in tracing the neurofunctional mechanisms underlying the differences in predictive styles existing in the general population. Crucially, an imbalance between alpha and theta synchronization leads to interindividual differences favoring priors overweighting (believers) vs. prioritization of sensory input (empiricist) strategy, respectively.

Highlights

- 1) Probabilistic prior shapes the decision criterion, not perceptual sensitivity
- 2) Shift in posterior alpha amplitude tracks the modulation in decisional bias
- 3) Parieto-occipital alpha coupling aids in biasing posterior alpha amplitude
- 4) Fronto-parietal theta coupling dampens the bias on posterior alpha amplitude
- 5) An imbalance between alpha vs theta coupling leads to different predictive strategies

Introduction

Perception goes beyond what hits the eyes and human decision does not result from a faithful integration of external inputs. According to predictive coding (Clark, 2013), they both emerge from an inferential-like process in which stimuli are conditionally interpreted considering prior and contextual information. This feature is able to explain several empirical evidence. For example, the presence of a stimulus is judged as a function of its probability of occurrence or recent sensory history (de Lange et al., 2018; Urai et al., 2019).

There are individual differences in the tendency to favor prior knowledge over incoming sensory evidence that explain heterogeneity in decision-making styles and underlie some psychopathological symptoms (Starita and di Pellegrino, 2018; Tarasi et al., 2022; Teufel et al., 2015). For example, recent empirical works have shown that strong predictive models can exert an undue influence on perceptual inferences causing hallucinatory phenomena (Corlett et al., 2019; Powers et al., 2017). Therefore, the process of exploiting prior knowledge needs to be monitored and controlled to ensure its adaptivity and flexibility. However, despite the role of predictive processing in explaining many decision-making phenomena and inter-individual differences in cognitive style, the understanding of the neural mechanisms involved is limited. Predictive coding states that models about the environment are processed by higher cortical areas and conveyed to lower-level regions for shaping the perceptual process (Boly et al., 2011; Rao and Ballard, 1999). At the electrophysiological level, these interactions would be carried out through phase synchronization of inter-area oscillatory activity (Engel et al., 2001; Fries, 2015, 2005). In particular, mounting evidence suggests that inter-regional alpha phase coupling is one of the ideal biological substrates for prediction conveyance given its role in neural information transfer (Arnal and Giraud, 2012): alpha oscillations carry the top-down signaling (Michalareas et al., 2016) and the strength of inter-areal alpha synchronization tracks the predictability of the stimulus (Bastos et al., 2020). The aim of this rhythmic transmission would be to regulate the activity of low-level areas by targeting markers involved in the modulation of decision outcomes, such as the amplitude of alpha oscillations (Di Gregorio et al., 2022; Samaha et al., 2020). Specifically, it is conceived that states of increased alpha power reflect a state of reduced neural excitability within and across participants (Romei et al., 2008b, 2008a), which in turn would inhibit stimulus processing (Jensen and Mazaheri, 2010; Klimesch et al., 2007). This hypothesis derives from a large body of studies reporting that increased alpha power in sensory regions is associated with reduced hit-rate (Romei et al., 2010; van Dijk et al., 2008) and number of phosphenes evoked by transcranial magnetic stimulation (Romei et al., 2008b, 2008a; Samaha et al., 2017a). However, the early findings were not able to disambiguate whether alpha fluctuations exert an influence on the objective ability to sample sensory stimuli [sensitivity (d')] or rather modulate response bias [criterion (c)]. Crucially, a recent study addressed this issue demonstrating that alpha amplitude modulations are associated with response bias and not sensitivity (Limbach and Corballis, 2016). Specifically, when pre-stimulus power is low, observers have a higher proneness to see a target (i.e., more liberal criterion), regardless of its actual presentation. Accordingly, several recent studies have shown that alpha amplitude modulates the tendency to report the presence of the target (Iemi et al., 2017), the confidence associated with the choice (Samaha et al., 2017b) and visual awareness (Benwell et al., 2021),

without affecting perceptual acuity. Nevertheless, the role of alpha in shifting the decision bias was mainly inferred by analyzing the relationship between spontaneous trial-by-trial fluctuations preceding the presentation of near-threshold stimuli and perceptual outcomes. It remains still unknown whether deliberate criterion modulation induced by prior information is supported by alpha shifting at the sensory areas level.

Furthermore, it is currently unclear which neural network would be accountable for the rhythmic transmission of prior-related information to the low-level areas. The parietal lobe may represent one of the seeds. Its activity has been associated with the extent to which the perceiver tuned its decision based on prior knowledge or task payoff (Hanks et al., 2011; Mulder et al., 2012; Platt and Glimcher, 1999; Rao et al., 2012). Moreover, rTMS over the right parietal cortex has been shown to disrupt the desynchronization of anticipatory alpha rhythms in the parieto-occipital cortex (Capotosto et al., 2009). In addition, alpha synchronization between parietal and visual cortex supports anticipatory visuospatial attention (D'Andrea et al., 2019; Siegel et al., 2008) by regulating alpha amplitude at posterior sites (Lobier et al., 2018). Here, in line with this evidence, we first decided to investigate whether alpha coupling between parietal and visual cortex could be responsible for predictive information signalling, by tuning the excitability of sensory cortices in a prior-dependent fashion.

Moreover, for predictive models not to override the information carried out by the sensory input, which may lead to dysfunctional processes such as hallucinatory phenomena (Powers et al., 2017), a supervisory system on the perceptual inference process could be conceived. Several lines of evidence would point to theta synchronization as a promising candidate crucially implicated in this monitoring process. Theta acts as an 'alarm signal', pointing to the need to engage cognitive control, whose implementation emerges from inter-site theta phase synchrony (Cavanagh and Frank, 2014). Indeed, theta has been shown to be involved in decisional adjustments (Cavanagh et al., 2009) through the functional interaction with posterior activity (Nurislamova et al., 2019), increasing when participants are induced to adopt a liberal criterion (Kloosterman et al., 2019) so as to prevent impulsive and biased responses (Cavanagh et al., 2013, 2011; Swart et al., 2018). Therefore, theta activity could underpin a higher-order mechanism subserved by a fronto-parietal executive network (López et al., 2019; Sauseng et al., 2005) that monitors the exploitation of predictive models.

In the current study, we explicitly probe these potential mechanisms by manipulating the expectation of target occurrence in a detection task with the aim of inducing response bias, while keeping sensitivity unchanged, to investigate 1) whether the alpha amplitude tracks the voluntary modulation of the decision

bias, 2) the differential role of neural coupling along the theta and alpha bands in preparing sensory areas activity to strategically shape perceptual decisions and 3) the role of these neural signatures in explaining individual differences in the handling of predictive information.

Materials and Methods

Participants

Sixty-eight participants (35 female; age range 18-35) signed a written informed consent prior to take part in the study, which was conducted in accordance with the Declaration of Helsinki and approved by the Bioethics Committee of the University of Bologna (protocol code 201723, approved on 26 August 2021).

Stimuli

Stimuli were presented on a 18" CRT display (Cathode Ray Tube, CRT, display resolution of 1280 x 1024 pixels, refresh rate 85 Hz) at a distance of 57 cm in a dimly lit room. Participants sat in a comfortable chair in front of the monitor. The stimuli were generated and presented using Matlab (version 2016, The MathWorks Inc., Natick, MA) and the Psychophysics toolbox. Visual stimuli were checkerboards appearing on the lower left visual field. The checkerboards presented could contain grey circles within each of the cells (target) or not (catch trials) (See figure S1). Participants were instructed to indicate via the keyboard the presence (by pressing key 'k' with the middle finger) or absence (by pressing key 'm' with the index finger) of the grey circles inside the checkerboard as quickly and as accurately as possible. Participants were instructed to give the response with their right hand to avoid confounding effects related to motor programming, as it was executed by the hemisphere opposite (i.e., the left) to the one responsible for sensory processing in the task (i.e., the right).

Experimental design.

The study was divided in two phases. In the first, each participant underwent an adaptive titration procedure to determine the contrast of the grey circles for which the detection accuracy was at ~ 70% when an equal number of target-present and target-absent trials (catch trials) was presented. We opted to include the presentation of catch trials to avoid confounding effects related to the difference response tendency adopted by the participants. In fact, by presenting only target-presence trials, it is not feasible to discriminate whether different threshold values depend on the effective perceptual ability since the absolute number of hit-rates

may vary significantly despite an equal sensitivity when controlling for the number of false alarms (Green and Swets, 1966). The second phase comprised 6 blocks of 90 trials each (Figure 1). Each trial started with the appearance of the probability cue presented at the center of the screen. The cue was presented for 1 s followed by a fixation dot. After a variable delay of 1.2–1.5 s a checkerboard containing (or not) grey circles at the titrated contrast within it appeared at the bottom left of the monitor for 60 ms. We opted to present the stimulus in only one hemifields to prevent spontaneous fluctuations in attention between the two hemifields in the prestimulus period from interfering with the results. Participants had to determine the presence or absence of the grey circles within the checkerboard and press the button associated with their choice. No timeout has been set for the response. After collecting the response, the screen appeared black for 1.9-2.4 s in the inter-trial interval. The cue was a rectangle with its bottom colored in red and its top colored in blue. The percentage of the red shading to the entire rectangle indicated the probability that the checkerboard contained the grey circles (target) within it. There were three level of cues. Cue high and cue low (informative cues) indicated the probability of the presence of the target of 67 and 33%, respectively. Instead, the neutral cue (un-informative cue) equally predicted (50%) the presence and absence of the target. The actual probability of target presentation was in accordance with the probability indicated by the cue. Participants were also explicitly told that the probabilistic cue was congruent with the actual probability of stimulus presentation.

Experimental paradigm

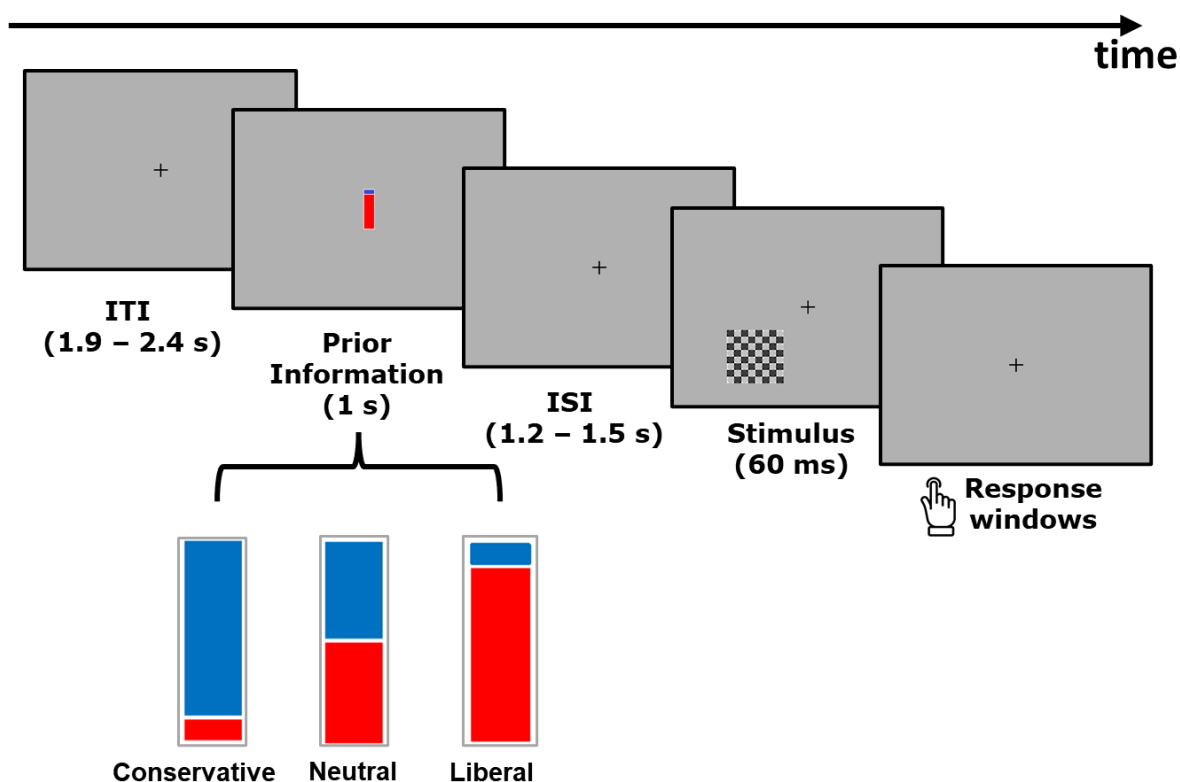


Figure 1. Experimental design. A. EEG data were collected during a simple visual detection task. Each trial started with a fixation cross, after which a probabilistic cue appears in the center of the screen. After this, a checkerboard containing (or not) grey circles at the titrated contrast within it appeared at the bottom left of the monitor for 60 ms. The cue was a rectangle with its bottom colored in red and its top colored in blue. The percentage of the red shading to the entire rectangle indicated the target-probability. There were three cue levels. The high and low probability cues indicated the probability of the presence of the target of 67 and 33%, representing the liberal and the conservative conditions, respectively. The neutral cue equally predicted the presence (50%) vs. absence (50%) of the target.

Signal-detection theory (SDT) modeling

We computed the SDT measures d' and c (Green and Swets, 1966). d' quantifies a participant's stimulus sensitivity (higher d' values are indicative of higher sensitivity), whereas c quantifies a subject's decision criterion (c value different from 0 implies the presence of choice bias). These measures were calculated based on the proportion of hits and false alarms. To evaluate the effect of the probabilistic cue on sensitivity and criterion, we computed d' and c separately for trials preceded by low, high, or neutral probability cues. To statistically investigate a cue-related effect on sensitivity and criterion, d' and c were subjected to a repeated-measures ANOVA with the cue type as within-factors (3 level: high, low and neutral probability). In order to interpret the results derived from the conducted ANOVA, post-hoc analyses were carried out using paired sample t-test by correcting the p-value for the number of comparisons made (p value corrected = 0.017). We have used customized functions taken from the gramm toolbox (Morel, 2018) for data visualization.

Drift diffusion modeling (DDM)

We fitted the drift diffusion model to RT distributions for 'stimulus presence'- and 'stimulus absence'-choices, separately for trials preceded by low, high, or neutral probability cues. We fitted the model using a hierarchical Bayesian parameter estimation of the Drift Diffusion Model using the HDDM toolbox (Wiecki et al., 2013). In HDDM, Bayesian inference through Markov chain Monte-Carlo (MCMC) sampling is used to approximate posterior distributions for each parameter at both the individual and group levels. The priors' distributions for each parameter were informed by a pool of 23 studies reporting the best fitting DDM parameters retrieved on a set of decision-making tasks (Matzke and Wagenmakers, 2009); see the supplement by (Wiecki et al., 2013) for visual representations of these priors. We initialized HDDM to draw 20000 posterior samples for each data with the first 2000 samples discarded as burn-in. We have fitted the model to RT distributions for 'stimulus presence'- and 'stimulus absence'-choices as opposed to the more common fits of correct and incorrect choice RTs to estimate the bias parameters (i.e., starting point $[z]$). In our fits, we allowed the following parameters to vary simultaneously according to probabilistic cue: (I) the mean drift rate (v); (II) the separation between both decision bounds (a); (III) the starting point of the accumulation process (z). We inspected traces of model parameters and their autocorrelation to ensure that the models had properly converged. We examined the overlap of the posterior distributions for the estimated

parameters, defining significance as less than 5% overlap. Because these are comparisons of Bayesian posterior distributions, we report the HDDM outcomes as q - rather than p -values. *To further evaluate the best-fit model, we performed posterior predictive checks, averaging 50 simulations generated by the posterior distribution of the fitted parameters, to verify the match between these simulated data sets and the actual data. Specifically, we first evaluated whether the reaction time pattern of the simulations reproduced that of the empirical data. In addition, we have ascertained through Pearson correlation analysis whether the average simulated response times were associated with the observed response times and whether the sensitivity/criterion indices calculated on the simulated data were matched to the actual values measured in the participants. Finally, we fitted an HDDM model using a simulated dataset as input to check the correspondence of the parameters extracted using the empirical data with those extracted from the simulated sample.*

EEG preprocessing and time frequency decomposition

Participants comfortably sat in a room with dimmed lights. A set of 64 electrodes was mounted according to the international 10–20 system. EEG signals were acquired at a rate of 1000 Hz and all impedances were kept below 10 k Ω . EEG was processed offline with custom MATLAB scripts (version R2021a) and with the EEGLAB toolbox (Delorme and Makeig, 2004). The EEG recording was filtered offline in the 0.5-100 Hz band and a notch-filter at 50 Hz was applied. The signals were visually inspected, and noisy channels were spherically interpolated. Epochs spanning –4100 to 2000 ms relative to checkerboard onset were extracted and individual trials were visually checked and those containing excessive noise, muscle or ocular artefacts discarded. An average of 470 trials per subject passed this stage. Next the recording was then re-referenced to the average of all electrodes, and we applied the Independent Component Analysis (ICA), an effective method largely employed for removal of EEG artefacts. Components containing artifacts that could be clearly distinguished from brain-driven EEG signals were subtracted from the data. After these steps, we downsampled the signals to 256 Hz and a Laplacian transform was applied to the data using spherical splines. The Laplacian is a spatial filter that aids in topographic localization by attenuating artifacts attributable to volume conduction, rendering the data more suitable for performing connectivity analyses. (Cohen, 2014). Subsequently, we implemented time-frequency analysis by convolving the time series data with a set of complex Morlet wavelets (whose cycles increased between three and eleven cycles as a function of frequency), defined as complex sine waves tapered by a Gaussian. Convolution was performed via frequency-domain multiplication, in which the Fourier-derived spectrum of the EEG data was multiplied by

the spectrum of the wavelet, and the inverse Fourier transform was taken. Then, we obtained the phase extracting the angle relative to the positive real axis and the amplitude by extracting the absolute value of the resulting complex time series. Amplitude was then condition-specific baseline-corrected using a decibel (dB) transform: $dB\ amplitude = 10 \times \log_{10}(amplitude / baseline)$. Baseline amplitude was defined as the average amplitude in the period ranging from -3100 to -2700 ms before stimulus onset.

EEG analysis - Oscillatory amplitude analysis

We focused the amplitude analysis on a cluster of central and right posterior electrodes (as the visual stimuli were presented in the left visual field) by averaging the amplitude of the following electrodes to avoid the potential issues inherent in selecting a restricted number of sensors: Oz, POz, Pz, O2, PO4, PO8, P2, P4, P6, P8. In order to specifically investigate the pre-stimulus oscillatory activity related to the prior use, a frequency per time nonparametric cluster-based permutation tests ($n = 1.000$) was performed on the amplitude difference between the high- and low- probability trials in all time points ranging from -600 to 0 ms relative to the checkerboard appearance by shuffling the type of trials for each individual for each permutation in order to create a dummy distribution of amplitude difference. This method is data-driven and allows to test point-by-point the significant differences between the two types of prior information in the entire time interval considered and for all the frequencies included controlling for multiple comparisons (Maris and Oostenveld, 2007). Furthermore, to check that the effects did not depend on the unequal number of trials in which the target was present in the different conditions, the above analyses were repeated by equating the number of trials by sub-sampling. Specifically, we subsampled an equal number of target trials and catch trials from each condition so that the number of trials per condition matched that in the condition of the fewest trials. Crucially, the pattern of results points in the same direction to that highlighted when considering the entire dataset (see supplementary materials, Figure S3A). Subsequently, we extracted, for each individual, the mean amplitude value of the time-frequency cluster resulted most significantly modulated by the prior (~8 - 14 Hz; ~ -400 - 0 ms). The difference between the amplitude values extracted in the conservative and the liberal trials (Δ amplitude) expresses the degree to which each participant regulates alpha pre-stimulus in a different way in the two conditions and was used in subsequent correlation analyses.

EEG analysis – brain-to-behavior analysis

To assess whether there was a relationship between the modulations at the behavioral level induced by the expectancy cue and the modulations at the oscillatory level, we conducted several correlation analyses. We

have taken the difference between the criterion (Δ criterion) adopted in conservative trials and the criterion adopted in liberal trials (i.e., $c_{cons} - c_{lib}$) as a proxy of criterion modulation (for a similar approach, see (de Lange et al., 2013). Analogously, in the Drift Diffusion domain, we have taken the difference between the starting point (Δ starting point) adopted in liberal trials and the starting point adopted in conservative trials (i.e., $z_{lib} - z_{cons}$) as a proxy of bias induction. The larger these shifts were, the more the subject adjusted their behavior based on the predictive cue. We have ascertained the presence of a relationship between these behavioural metrics and the alpha modulation in cue low- vs high- expectancy trials by computing Pearson (r_p) and Spearman (r_s) correlations between Δ amplitude and Δ criterion as well as between Δ amplitude and Δ starting point. Moreover, we have run the skipped, both Pearson ($r_{p\ skipped}$) and Spearman ($r_{s\ skipped}$), correlation to ascertain the robustness of the association using the Robust Correlation toolbox (Pernet et al., 2013) conducting null hypothesis statistical significance testing using the non-parametric bootstrap percentile test (2000 samples, 95% confidence interval, corresponding to an alpha level of 0.05). With this method, outliers are removed guaranteeing a more robust estimate of the association between the variables under consideration. As a control analysis, we used the same correlational approach to assess any association between the difference in alpha amplitude and the difference in d' ($d_{cons} - d_{lib}$) and drift rate ($v_{lib} - v_{cons}$) in the two conditions. Both Pearson's and Spearman's correlations, as well as the skipped correlations, found no association between alpha adjustment and the difference in objective performance indices in the conservative vs. liberal trials (all $p > .52$).

EEG analysis – Functional connectivity

Functional interactions between oscillatory activity were captured by quantifying the inter-areas phase relationship. Specifically, we used the weighted phase lag index (wPLI) (Vinck et al., 2011) to evaluate the degree of synchronization between the signals. wPLI is based on the phase lag index (PLI) (Stam et al., 2007), which defines connectivity as the absolute value of the average sign of phase angle differences (+1 or -1, relative to the real axis). In contrast to the PLI, however, wPLI gives maximal weighting to phase differences that are far from the real axis, and hence omits all signals associated with artificial synchrony/volume conduction. wPLI values range between zero (random relationship between phases) and one (total phase synchronization). Phase connectivity was estimated in the pre-stimulus time (~ -600 to 0 ms) in the theta (~5-8 Hz) and in the alpha (~8-14 Hz) frequency band. We grouped the electrodes into 3 regions of interest (ROIs) in the right hemisphere going from rostral to caudal (frontal, parieto-central and occipital) by relying on the nomenclature of the International Standard 10-20 system, which associates labels

with electrodes according to the cortical area on which they are situated. The frontal ROI comprises: FC2, FC4, FC6, FT8, F2, F4, F6, F8 electrodes. The parieto-central ROI comprises: Pz, P2, P4, P6, P8, CP2, CP4, CP6 electrodes. The occipital ROI comprises: Oz, O2, POz, PO4, PO8 electrodes. We selected a consistent number of sensors to be included in each ROI to avoid the potential pitfalls inherent in selecting a limited number of electrodes on which to perform analyses. We statistically evaluated whether prior knowledge was reflected by changes in pre-stimulus brain connectivity in the fronto-parietal and parieto-occipital network using an approach similar to Alekseichuk et al., (2016). The method employed is data-driven and allows to test electrodes-by-electrodes the significant differences between the two types of prior information in the synchronization index controlling for multiple comparisons (critical alpha = 0.05). First, we conducted, for each electrode's pairs within the investigate ROIs, a paired t-test to compare weighted phase-lag index between the conservative vs liberal condition. The connectivity index was then estimated for every condition as follows: $CI = \frac{sp_sig}{sp_total}$, where sp_sig is the number of sensor pairs that demonstrates the significant modulation of connectivity between the two conditions and sp_total is the total number of sensor pairs considered. A permutation test was then introduced to estimate the level of significance. To this end, for each individual, the wPLIs values associated with the two conditions (i.e., liberal and conservative) were randomly permuted to generate dummy data. These data entered the analysis as described above. The procedure was repeated 1.000 times, and the resulting distribution of the dummy connectivity indices was used to estimate the 95% confidence interval; if the connectivity indices calculated on the real data exceeded this interval, they were considered statistically significant. This procedure was carried out separately for the two-frequency band (i.e., theta and alpha) and for the two networks (i.e., fronto-parietal and parieto-occipital) considered.

Investigate the relation between connectivity indices and amplitude modulations

Since we hypothesize that the synchronization along the fronto-parieto-occipital axis was crucial to shape the activity at the level of sensory cortex, we assessed whether the changes in connectivity indices observed in the fronto-parietal and parieto-occipital networks were associated with the prior-related alpha amplitude modulation. First, we hypothesized that the differentiation observed in parieto-occipital alpha coupling between conservative and liberal conditions would support a rhythmic modulation of sensory excitability to predispose perception. Thus, we extracted, for each participant, the mean wPLI values of the significant connections (sp_sig) along the parieto-occipital circuit that emerged from the previously conducted analysis. Next, we took the difference between the extracted wPLI values in the conservative - liberal conditions (Δ alpha coupling) as

predictors of pre-stimulus alpha amplitude modulation (Δ amplitude). Secondly, we asserted that fronto-parietal theta synchronization would represent a predictive control mechanism that set the perceptual areas in an unbiased state. Therefore, we expected that the increased fronto-parietal theta synchronization observed in liberal vs. conservative trials underlies reduced pre-stimulus alpha amplitude differentiation between conditions. Thus, we extracted, for each individual, the mean wPLI values of the significant pairwise connections (*sp_sig*) along the fronto-parietal circuit that emerged from the previously conducted analysis. Next, we took the difference between the extracted wPLI values in the liberal - conservative conditions (Δ theta coupling) as predictors of pre-stimulus alpha amplitude modulation (Δ amplitude). We have ascertained the presence of a relationship between Δ alpha connectivity and Δ alpha amplitude as well as between Δ theta connectivity and Δ alpha amplitude by computing Pearson and Spearman correlations. Moreover, we have runned the parametric skipped (both Pearson and Spearman) correlation to ascertain the robustness of the association using the Robust Correlation toolbox (Pernet et al., 2013) conducting null hypothesis statistical significance testing using the non-parametric bootstrap percentile test (2000 samples, 95% confidence interval, corresponding to an alpha level of 0.05).

Individual differences in predictive style are predicted by synchronization along the rostro-caudal axis

To investigate whether a differential weight assigned to the outlined neurofunctional mechanisms might underpin the differences in predictive style adopted, we used a median split approach to separating individuals that showed large (vs. low) prior-based pre-stimulus differentiation in alpha amplitude.

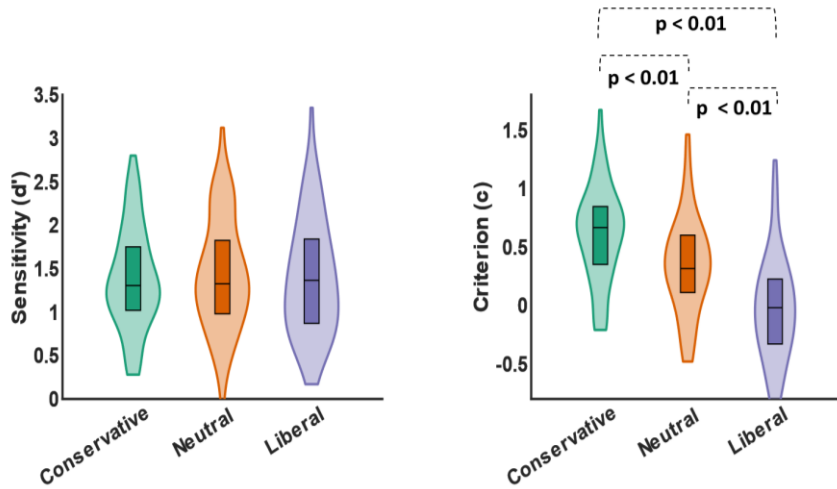
Specifically, we have calculated the median of Δ alpha amplitude index (median = 0.12) that aided us to divide the subjects in two groups: the high alpha amplitude modulators (i.e., individuals which show above-median Δ alpha index) and low alpha amplitude modulators (i.e., individuals which show below-median Δ alpha index). To assess whether the two groups showed specific differentiation related to criterion shift, we assessed with an independent samples t-test whether the Δ criterion index was different in the two groups. As a control analysis, we tested whether the two groups showed differentiation in discriminative ability. To this end, we used an independent-samples t-test with dependent variable the overall d' of the participants (the cue factor was collapsed since previous analyses clarified its nonimpact on sensitivity). Furthermore, to ascertain the relationship between the modulation of connectivity indices along the rostro-caudal axis and the inter-individual difference in the shaping of alpha amplitude due to the prior knowledge, we conducted two ANOVAs. As dependent variable, we extracted, at the individual level, the mean wPLI values of the pairwise connections (*sp_sig*) that exceeded the significance threshold in the previously conducted non-

parametric analysis. Since there were two significant prior-related effect on connectivity metrics (i.e., theta in the fronto-parietal network and alpha in the parieto-occipital network), we conducted two mixed ANOVAs. Both ANOVAs take into account a between-subjects independent variable, the group type (two levels: high vs low alpha modulators), and a within-subjects independent variable, the trial type (liberal vs conservative). In order to interpret the results derived from the conducted ANOVAs, post-hoc analyses were carried out using t-test by correcting the p-value for the number of comparisons made (4 comparison, p value corrected = 0.0125).

Results

Human participants (n = 68) performed a simple detection task. In each trial, a checkerboard was presented on the lower left visual field. The checkerboards presented could contain isoluminant grey circles within each of the cells (target) or not (catch trials). Participants were instructed to indicate via the keyboard the presence vs. absence of the target. In the first phase, each participant underwent an adaptive titration procedure to determine the contrast of the grey circles for which the detection accuracy was at ~ 70%. The overall accuracy value in the main task was close to 70% (namely, 71.9%), testifying to the effectiveness of the titration phase. In the second phase, the checkerboards were preceded by a symbolic cue indicating the probability of the target's presence. There were three cue levels. The high and low probability cues indicated the probability of the presence of the target of 67 and 33%, representing the liberal and the conservative conditions, respectively. The neutral cue equally predicted the presence (50%) vs. absence (50%) of the target. The actual probability of target presentation was in accordance with the probability indicated by the cue. Participants were also explicitly told that the probabilistic cue was congruent with the actual probability of stimulus presentation.

A. Signal Detection Theory (SDT)



B. Reaction times distribution

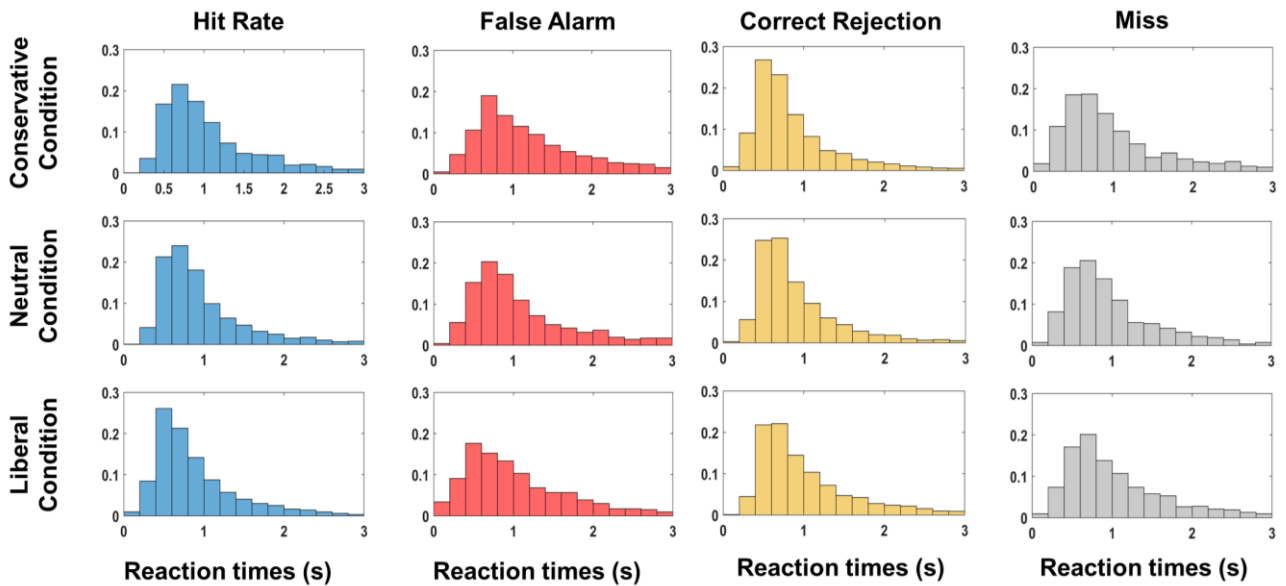


Figure 2.

- A. *Signal Detection Theory. Sensitivity (d') and Criterion (c) indices are represented separately for trials preceded by low, high, or neutral probability cues. Prior information had no effect on sensitivity. In contrast, the probabilistic cue significantly shapes the decision criterion: a more liberal criterion was adopted when trials were preceded by high probability cue relative to both trials preceded by neutral and low probability cue, whereas the criterion was more conservative when low probability cue precedes the checkerboard appearance relative to neutral cue.*
- B. *RT distributions of hit rates, false alarms, correct rejections, and misses are shown in the panels.*

The reaction times were grouped into 15 bins starting at 0 and ending at 3s, each of which considers an interval of 0.2 s. The height of each bin represents the density of observations in that interval.

By qualitative inspection of the graphs, there is an acceleration effect of both the accurate and inaccurate response if they are congruent with the prior. For example, there are faster hit rates in the liberal condition matched by faster false alarms. Conversely, in the conservative condition, there are faster correct rejections as well as faster misses.

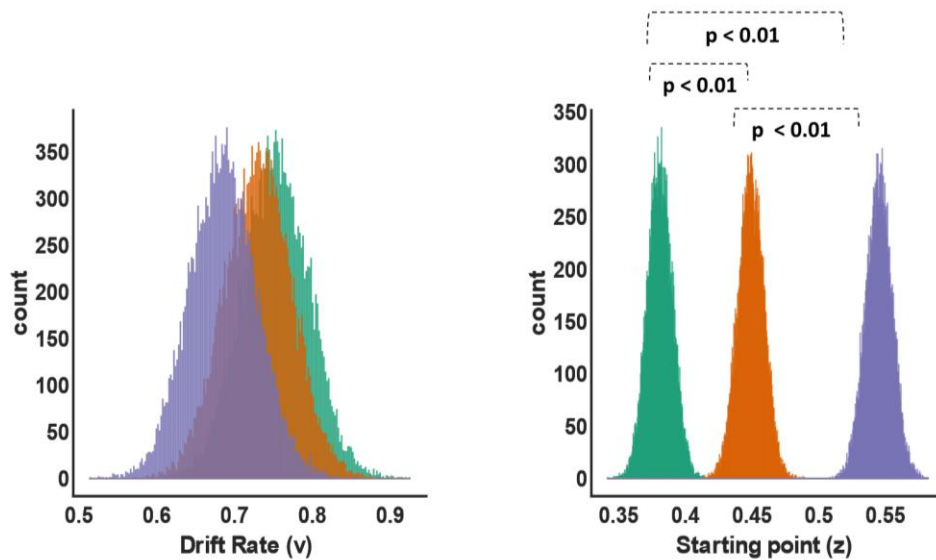
Prior information modulates the decisional bias

We computed the signal detection theory indices d' (sensitivity) and c (criterion) (Green and Swets, 1966) separately for trials preceded by low, high, or neutral probability cues (Figure 2A). The conducted repeated-measures ANOVA did not find any impact of probabilistic cue on sensitivity ($F_{2,134} = 1.13$; $p > 0.32$). In contrast, the cue significantly shapes the decision criterion ($F_{2,134} = 107.44$; $p < 0.01$): a more conservative criterion was adopted when trials were preceded by low probability cue ($c_{\text{low}} = 0.61 \pm 0.05$) relative to both trials preceded by neutral cue ($c_{\text{mid}} = 0.34 \pm 0.05$; $t_{67} = 7.4$, $p < 0.01$) and high probability cue ($c_{\text{high}} = -0.03 \pm 0.05$; $t_{67} = 11.14$, $p < 0.01$), whereas the criterion was more liberal when high probability cue precedes the checkerboard appearance relative to neutral cue ($t_{67} = -10.91$, $p < 0.01$). Focusing on the distribution of reaction times (Figure 2B, Table S1), it can be observed that expectation-like information prioritizes congruent decision outcomes rather than accelerating correct/wrong responses. For example, hit rates are faster in the liberal trials than in the other conditions, but this is coupled with the presence of faster false alarms. A Bayesian parameter estimation of the Drift Diffusion Model parameters using the HDDM toolbox (Wiecki et al., 2013) (Figure 3A) confirm these patterns of results: the posterior distributions revealed higher starting point in the high probability trials relative to both mid probability trials ($q < 0.01$) and low probability trials ($q < 0.01$) and lower starting point in the low probability trials relative to mid probability trials ($q < 0.01$). No difference was found both in drift rate and in threshold separation (all $q_s > 0.05$). This implies that the speed of accumulation (v) and the amount of evidence that needs to be accumulated until a decision is taken (a) do not differ according to conditions. We also confirmed the goodness of the fitting procedure. Specifically: 1) the pattern of simulated response times with posterior prediction check were very similar to those empirically collected (Fig. 3B); 2) the simulated mean response times were correlated with the observed response times ($r = .97$; $p < .01$, Fig. S2A); 3) the sensitivity/criterion indices calculated on the simulated data were significantly associated with the actual values measured in participants (Fig. S2B); 4)

there were no significant differences between real vs. estimated DDM parameters using a simulated sample (all $q_s \geq .17$), which are further found to be strongly associated (Fig. S2C). Therefore, both posterior predictive checks and correlation analyses suggested that the model fit the data properly.

Overall, the behavioral results indicate that the experimental paradigm used was able to manipulate response bias without affecting other decision-making parameters.

A. Drift Diffusion Model (DDM)



B. Empirical RT vs Fitted RT

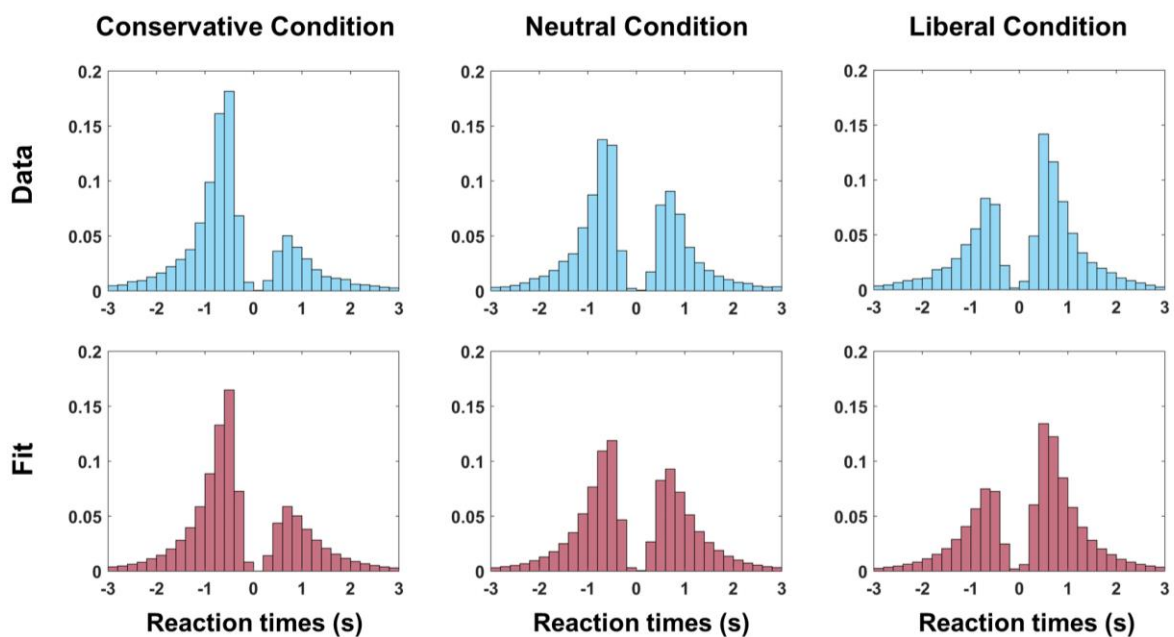


Figure 3.

- A. *Drift Diffusion Model. A Bayesian parameter estimation of the Drift Diffusion Model parameters revealed the presence of higher starting point in the liberal relative to both neutral and conservative trials and lower starting point in the low probability trials relative to mid probability trials. No difference was found in the drift rate parameter.*
- B. *The upper panel shows the distribution of the empirical RTs under the three experimental conditions, while the lower panel shows the distribution of the simulated RTs using the fitted parameters. The reaction times were grouped into 30 bins starting at -3s and ending at 3s, each of which considers an interval of 0.2s. The height of each bin represents the density of observations in that interval. The RT distribution for no target response is plotted negatively, so the RT distribution for no target presence response trials is given on the left side of zero, while the distribution for target presence response trials is shown on the right side of zero. In general, we can see that no target presence response is overrepresented in the conservative condition, while target presence response become the majority in the liberal condition. Notably, the empirical and simulated data show extremely similar and overlapping trends, testifying to the goodness of fit obtained with the HDDM model.*

Pre-stimulus alpha oscillations affect perceptual bias

We assessed whether preparatory activity in the posterior regions was modulated by prior information by running a frequency per time non-parametric permutation test on the amplitude difference between the liberal and the conservative trials across the 600-millisecond pre-stimulus window and a broad range of frequencies (2–50 Hz). The conducted analysis revealed a significant effect in the pre-stimulus period, particularly pronounced in the alpha range (Figure 4A). Specifically, there was greater amplitude suppression in the liberal relative to the conservative condition. To demonstrate the spatial specificity of this neural effect, we conducted a control analysis to ascertain whether there was a similar modulation of the time-frequency representation in the left posterior electrodes. The cluster-based analysis did not reveal the presence of significantly different clusters that distinguished the liberal from the conservative condition. Furthermore, to mitigate the possibility that the effect was due to a choice-predictive motor activity (Donner et al., 2009), we assessed whether there was a differentiation in the time-frequency representation in the sensors representing the motor areas activity [electrodes C1 and C3 (Shibata et al., 2021; Thut et al., 2000)]. Again,

the conducted analysis did not individuate any clusters that differentiated the two conditions. In addition, to further confirm the spatial specificity of the neural effects, we have depicted (Figure 4B) the topography of the differential pre-stimulus activations between the liberal and conservative condition in the alpha range. The posterior areas, especially those located to the right hemisphere, are the only showing consistent pre-stimulus differentiation between the conditions, testifying to the presence of spatial segregation of the effects.

Next, we analyzed the functional significance of this neural differentiation. If, as hypothesized, the highlighted voluntary modulation of the amplitude of alpha fluctuations is linked to prior-dependent behavioral changes, it is reasonable to expect an association with response bias. Indeed, Pearson and Spearman's correlation analyses showed a positive correlation between Δ criterion (i.e., how much individual shift the criterion) and Δ alpha amplitude (i.e., how much individual shift the alpha amplitude) ($r_p = .32$, $p < 0.01$; $r_p \text{ skipped} = 0.35$, $CI = [0.15 \ 0.49]$; $r_s = .38$, $p < 0.01$; $r_s \text{ skipped} = 0.41$, $CI = [0.16 \ 0.56]$; Figure 4C) as well as between Δ starting point (i.e., how much individual shift the starting point) and Δ alpha amplitude ($r_p = .26$, $p < 0.05$; $r_p \text{ skipped} = 0.37$, $CI = [0.17 \ 0.55]$; $r_s = .3$, $p = 0.01$; $r_s \text{ skipped} = 0.39$, $CI = [0.18 \ 0.58]$). These findings showed that alpha modulation is linked to the shaping of subjective response criterion as well as with a shifting of the starting point of the accumulation process congruent with the probabilistic information received. Specifically, the greater the alpha amplitude adjustment, the greater the response bias triggered. Thus, these results suggested that alpha amplitude regulation is a crucial marker of response strategy tuning. Furthermore, the relationship between the magnitude of alpha and the criterion adopted is present beyond the condition considered, with higher alpha associated with a more conservative criterion in both the liberal and conservative conditions (see supplementary materials, S3B).

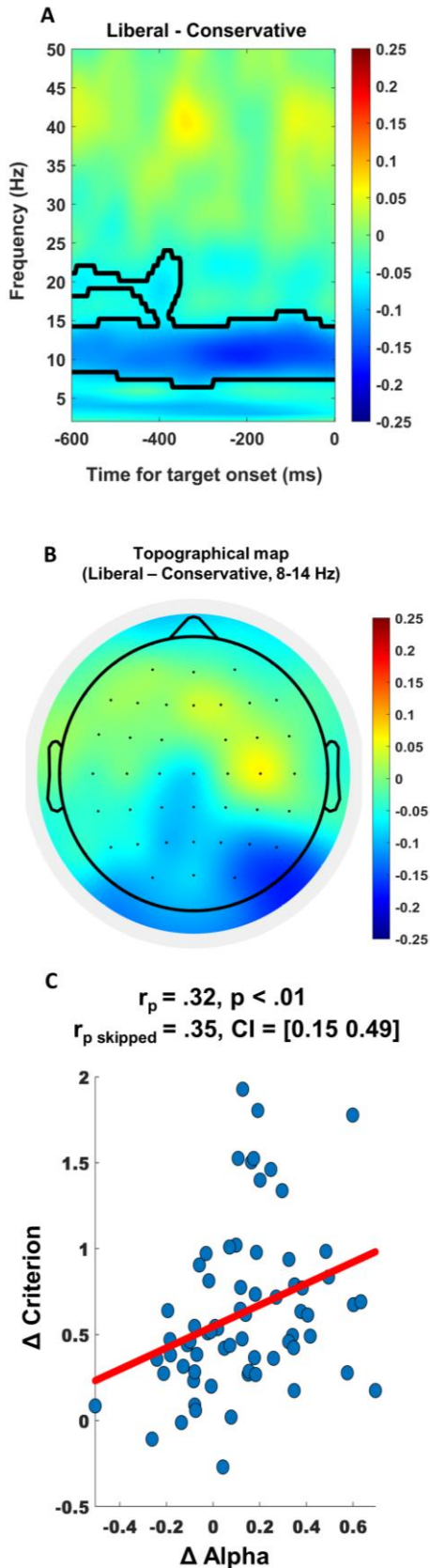


Figure 4. Alpha amplitude tracks perceptual bias.

A. Time-frequency map of the pre-stimulus (-600, 0 ms) amplitude difference between liberal and conservative trials registered in regions involved in visual processing. Time 0 refers to stimulus onset. Black contours denote cluster resulting significant from statistical analysis. It is noticeable a reduction in the pre-stimulus alpha amplitude in the liberal vs. conservative conditions, prominently in the alpha band.

B. Topography of the differential activations between the liberal and conservative condition in the alpha range (8-14 Hz) in the pre-stimulus window (-600 - 0 ms). Oscillatory activity in the alpha band diverges in the two conditions precisely in the posterior electrodes and peaks predominantly in the right hemisphere. The rest of the brain activations appear comparable in magnitude. This indicates a spatially localized effect that prepares cortical activity specifically in regions dedicated to stimulus detection.

C. Association between behavioral and neural markers of prior information. It is observable a significant positive correlation between individual differences in prestimulus alpha amplitude between conservative and liberal trials (Δ amplitude) and the behaviorally prior-induced criterion shift (Δ criterion).

Inter-areas couplings in theta and alpha bands shape predictive processes

Next, we evaluated the neurofunctional role of fronto-parietal-occipital interplay in theta and alpha bands in predictive processing. Functional interactions between oscillatory activity were captured by quantifying the phase relationship between the neural signals using the weighted phase lag index (wPLI) (Vinck et al., 2011). The non-parametric analysis conducted showed that the connectivity index (CI), which expresses the proportion of sensor pairs exhibiting a significant difference in connectivity between liberal and conservative trials, showed a clear differentiation between conditions and networks (Figure 5). Regarding the fronto-parietal network, the permutation test indicated that $CI = 0.094$ corresponds to the 5% significance level. Accordingly, there is a significant increase in theta connectivity in the liberal condition compared to the conservative condition ($CI_{\theta \text{ liber.} > \theta \text{ cons.}} = 0.156$) while all other comparisons do not exceed the threshold value (all $CI < 0.032$). A diametric pattern of results emerged when considering the synchronization along the parieto-occipital circuit in which the permutation test indicated that $CI = 0.1$ corresponds to the 5% significance level. Indeed, the conducted analysis showed increased alpha synchronization when participants expected a low vs. high probability of stimulus presence ($CI_{\alpha \text{ cons.} > \alpha \text{ liber.}} = 0.125$). No other comparisons within the parieto-occipital network exceeded the threshold value (all $CI = 0$). Furthermore, we ruled out (see supplementary materials, Figure S4) that the synchronization effect could be explained by the simultaneous increase in the amplitude of alpha oscillations in the conservative condition.

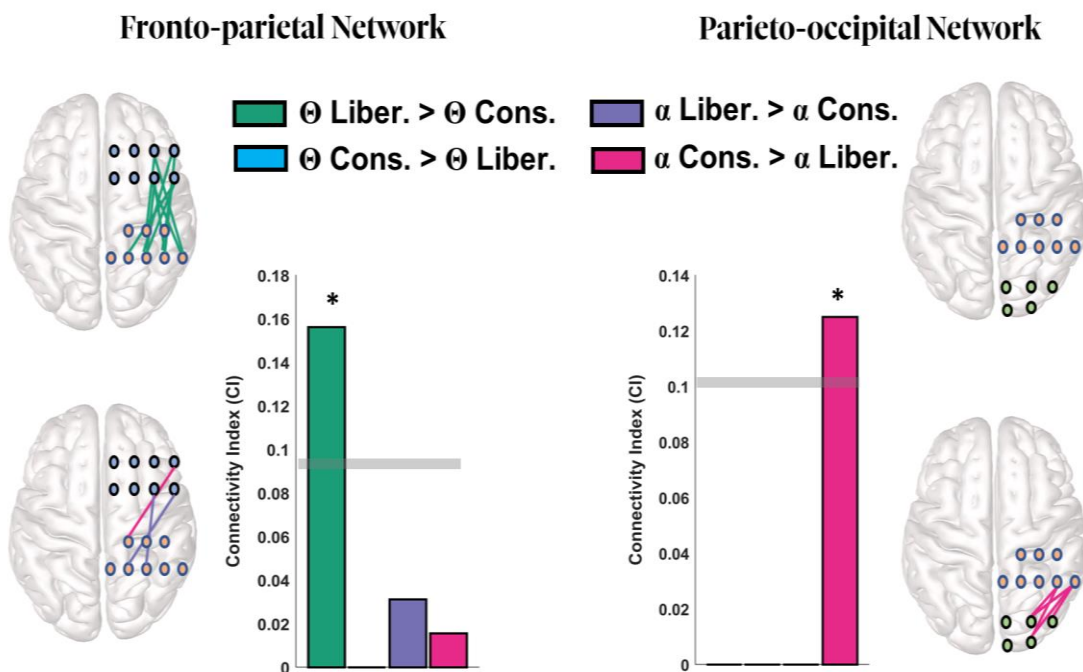


Figure 5. Fronto-parietal-occipital interplay in theta and alpha bands is shaped by predictive processing.

A. In the fronto-parietal network, theta coupling is enhanced in the liberal condition compared to the conservative condition while all other comparisons do not exceed the threshold value (gray line denotes the level of statistical significance).

B. In the parieto-occipital network, alpha coupling is enhanced in the conservative condition compared to the liberal condition while all other comparisons do not exceed the threshold value (gray line denotes the level of statistical significance).

Subsequently, we assessed the functional role of these inter-area dynamics. Recent evidence posits that high-level predictive information is transmitted across the alpha band to influence simpler processes occurring at earlier hierarchical nodes (Bastos et al., 2020). Thus, we argued that the differentiation observed in alpha coupling between conservative and liberal conditions would support a rhythmic modulation of sensory excitability to predispose perception. Specifically, the greater the increase in parieto-occipital synchronization in conservative vs liberal trials, the more there is a congruent shift in cortical excitability indexed by alpha amplitude regulation. The correlational analysis conducted (Figure 6) confirmed this assumption highlighting a significant relationship between alpha coupling shift and alpha amplitude regulation ($r_p = .26, p < 0.05$; $r_{p \text{ skipped}} = .37, CI = [0.12 \text{ } 0.56]$; $r_s = .27, p < 0.05$; $r_{s \text{ skipped}} = .35, CI = [0.11 \text{ } 0.56]$). Specifically, the more the participants showed increased alpha coupling in the conservative compared with the liberal condition, the more their pre-stimulus alpha amplitude was modulated in a prior-dependent fashion (i.e., higher in the conservative condition, lower in the liberal condition). In contrast, we hypothesize that fronto-parietal theta synchronization would represent a complementary process that controls the predictive process by setting the visual cortex in an un-biased state that allows for a more veridical representation of the external world. Therefore, we expect that the increased theta synchronization observed in liberal vs. conservative trials underlies reduced pre-stimulus alpha amplitude differentiation between conditions. Indeed, the correlational analysis conducted (Figure 6) showed that the increased theta synchronization observed in the liberal vs. conservative condition was associated with reduced pre-stimulus alpha amplitude regulation ($r_p = -.28, p < 0.05$; $r_{p \text{ skipped}} = -.37, CI = [-.55 \text{ } -0.16]$; $r_s = -.3, p = 0.01$; $r_{s \text{ skipped}} = -.3, p = 0.01$;

skipped = - .35, CI = [-.56 -.13]). Specifically, the more individuals increased coupling in theta in the liberal compared to conservative trials, the less differentially visual cortices responded to probabilistic information prior to target onset.

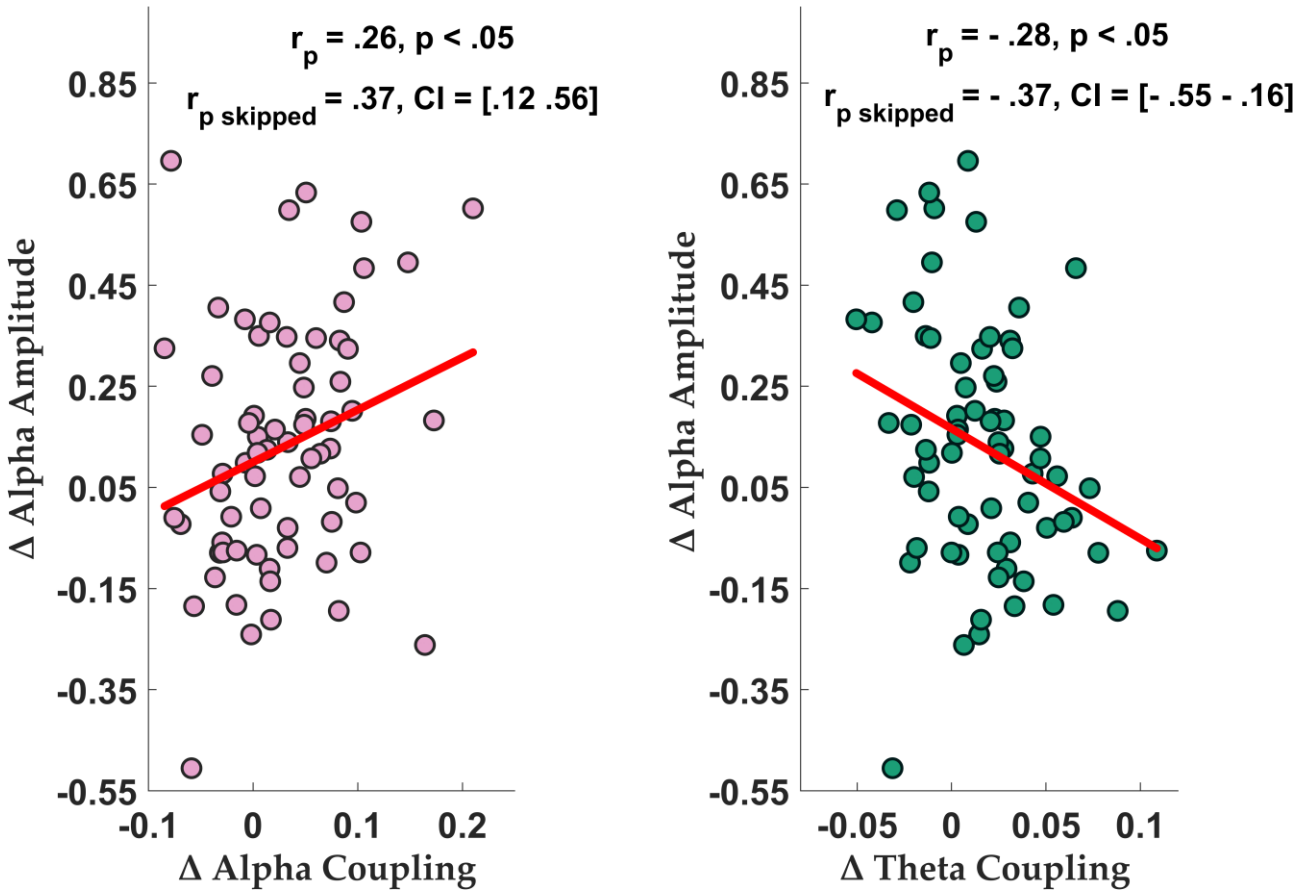


Figure 6. Alpha and theta synchronization play a diametrical role in cortical excitability setup.

A. Association between parieto-occipital alpha coupling and alpha amplitude regulation. It is observable a significant positive relationship between alpha coupling shift and alpha amplitude modulation. Thus, the increased alpha alignment in the conservative vs. liberal condition supports the priors-dependent modulation of pre-stimulus alpha amplitude.

B. Association between fronto-parietal theta coupling shift and alpha amplitude regulation. It is observable a significant negative relationship between theta coupling shift and alpha amplitude modulation. Thus, the increased theta synchronization in the liberal compared to conservative trials subtends a lower prior-based differentiation of posterior cortex excitability.

Synchronization along the rostro-caudal axis accounts for individual differences in sensory bias setting

The analyses conducted showed that alpha and theta synchronization play a diametrical role in cortical excitability setup. The presence of neural phenomena that facilitate vs. dampen predictive processing couples well with behavioral and computational evidence showing significant interindividual differences in prediction handling (Tulver et al., 2019). Indeed, people could be distributed within a predictive continuum at the poles of which are placed individuals who make an overuse (vs. underuse) of predictive information (Tarasi et al., 2022). Thus, we hypothesized that the different weight assigned to the outlined neurofunctional mechanisms might underpin the differences in predictive style adopted. Specifically, individuals who tend to modulate sensory cortex activity more according to priors (prior-prone individuals) would be dominated by the alpha-based prediction transmission mechanisms, whereas individuals who tend to discount predictive information (prior-resistant individuals) would place the areas involved in stimulus encoding in a neutral state of expectation through strong regulation of theta coupling. To test this hypothesis, we have used a median split approach by subdividing the participants in two groups based on their (prior-based) alpha amplitude modulation (Δ alpha amplitude). We would expect a differential connectivity pattern in subjects who heavily adjust visual cortex excitability (High Modulators) as a function of the prior knowledge compared to those who show less modulation (Low Modulators). According to these premises, above-median alpha amplitude modulators should be associated with a higher modulation of alpha coupling, whereas below-median alpha amplitude modulators should exhibit a higher regulation of fronto-parietal theta communication. First, we replicated the relevance of alpha modulation specifically in the change of criterion since the high- alpha modulators (Δ criterion_{high alpha modulators} = 0.80 ± 0.09) show greater shift in the bias measures relative to low-alpha modulators (Δ criterion_{low alpha modulators} = 0.46 ± 0.06 , $t_{66} = 3.23$, $p < 0.01$), while no difference in perceptual sensitivity can be tracked in the two groups (d' _{high alpha modulators} = 1.39 ± 0.09 ; d' _{low alpha modulators} = 1.40 ± 0.11 ; $t_{66} = 0.06$, $p > 0.96$). Furthermore, the conducted ANOVA proved the presence of a significant interaction term between trials type (liberal vs conservative) and group (low- vs high- modulators) when considering the fronto-parietal theta connectivity ($F_{1,66} = 8.47$, $p < 0.01$). Post-hoc analysis revealed that, while the low-alpha modulators group showed enhanced synchronization in the liberal relative to conservative condition (liberal = 0.16 ± 0.01 , conservative = 0.13 ± 0.01 , $t_{33} = 4.73$, $p < 0.01$), the high-alpha modulators showed a comparable level of coupling in the two types of trials (liberal = 0.14 ± 0.01 , conservative = 0.13 ± 0.01 , $t_{33} = 1.39$, $p > 0.17$). A different pattern of results emerged considering the parieto-occipital alpha connectivity. Indeed, the conducted ANOVA replicated the presence of a significant

interaction term between trials type and group ($F_{1,66} = 4.30$, $p < 0.05$) and highlighted the significance of the group factor ($F_{1,66} = 7.24$, $p < 0.01$). Post-hoc analyses revealed the presence of a general increase in alpha connectivity in the high modulator group (Conservative trials: high modulators = 0.36 ± 0.03 , low modulators = 0.26 ± 0.02 , $t_{66} = 2.95$, $p < 0.01$; Liberal trials: high modulators = 0.32 ± 0.02 , low modulators = 0.24 ± 0.02 , $t_{66} = 2.30$, $p < 0.05$), which also increased synchronization on conservative trials compared with the liberal condition ($t_{33} = 3.95$, $p < 0.01$), whereas the low-modulators show no differentiation between the two conditions ($t_{33} = 1.44$, $p > 0.16$). These results demonstrated that the synchronization along the fronto-parietal-occipital axis is associated to inter-individual differences in perceptual bias setting. Specifically, modulation in theta connectivity is associated with a lack of expectancy-dependent bias in pre-stimulus activity. Conversely, individuals which showed greater prior-based regulation of visual cortex excitability are characterized by the presence of a significant modulation in alpha phase synchrony. Overall, these results suggest that the phase aligning along the alpha and theta bands mediates frequency-specific dissociated processes on posterior alpha amplitude that could underpin the differential use of probabilistic models in individuals within the general population (Figure 7).

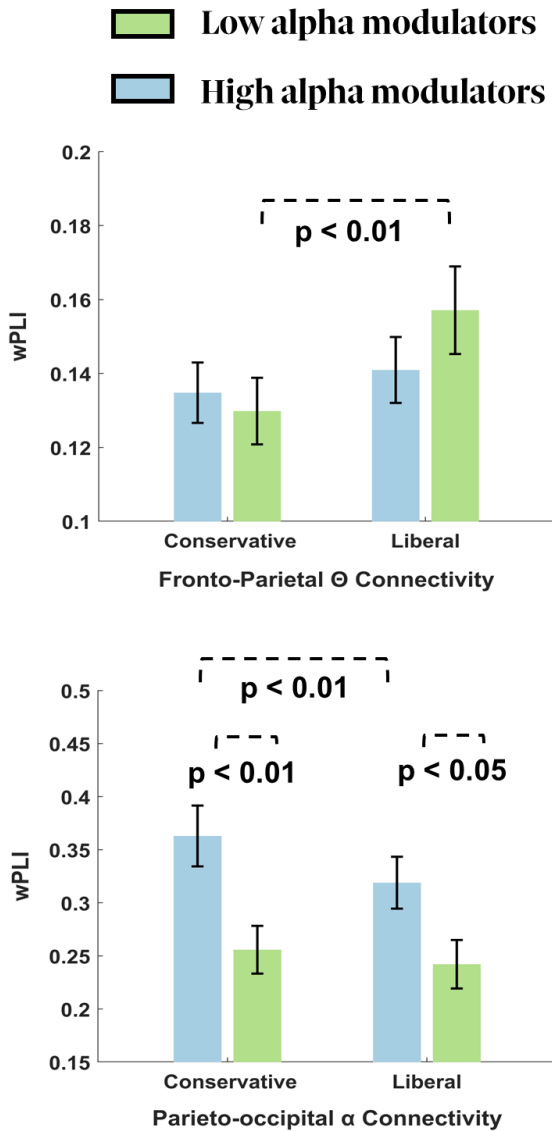


Figure 7. Synchronization along the rostro-caudal axis accounts for interindividual differences in predictive style.

A. Individuals who weakly set the posterior alpha amplitude as a function of expectation showed reduced response bias and increased fronto-parietal theta synchronization in the liberal compared to conservative condition.

B. Participants characterized by greater alpha amplitude regulation showed large criterion shift paired with a general increase in parieto-occipital coupling in the alpha band and enhanced alpha synchronization in conservative vs liberal trials.

Discussion

To investigate the behavioural and neural correlates of the predictive processing in the visual modality, we recorded the brain activity of human observers while performing a probabilistic detection task. Behavioural results indicate that participants were able to incorporate expectation-related information into their decision-making process. Specifically, the manipulation of perceptual expectations was able to elicit a response bias (i.e., shaping the *criterion* and *starting point*) while leaving the objective performance (i.e., *d-prime* and *drift rate*) unchanged. At the neural level, the perceptual prior resulted in a change in posterior alpha oscillatory

pattern along with a reconfiguration of long-range connectivity in the rostro-caudal axis in the alpha and theta bands.

Prior information plays a key role in optimising perceptual decision making. However, it was not clear whether the functional role of expectations is to increase perceptual sensitivity to the expected stimuli or to influence what is perceived. Literature studies indicate that priors affect response rate (Bang and Rahnev, 2017), reaction times (Mulder et al., 2012), and metacognition (Sherman et al., 2015) but have a negligible (Wyart et al., 2012) or even detrimental effect on perceptual sensitivity (Rahnev et al., 2011). The behavioural results described strengthen the idea that expectations drive the content of perception: providing the probability of target-presence induces the participant to respond congruently to the prior information received regardless of the objective occurrence of the stimulus. At the neural level, the induction of response bias was reflected in the change in pre-stimulus alpha amplitude. Alpha rhythm is a key predictor of trial-by-trial variability in decision outcomes (Di Gregorio et al., 2022; Samaha et al., 2020). Indeed, spontaneous alpha suppression has been related to increased tendency to report the presence of the target, even when no stimulus was presented (Iemi et al., 2017; Limbach and Corballis, 2016). The results of the presented study extend this range of findings as it shows that alpha oscillations are also implicated in voluntary modulation of the decision criterion. Indeed, an increased anticipation of target-presence is associated with a greater suppression of the amplitude of pre-stimulus alpha oscillations. Crucially, the differentiation of alpha wave amplitude in the liberal vs. conservative condition was associated with the magnitude of change in the criterion at the individual level. Thus, this biological marker appears to be related to the choice bias induced on the behavioural side. Furthermore, this result prompts the question of how much the fluctuation in pre-stimulus alpha amplitude highlighted in previous literature reflects a trial-by-trial variations in self-generated expectations about the presence of the stimulus in the upcoming trial rather than a stochastic process. It should be noted that the highlighted neural effects emerge considering the sensors placed in the right hemisphere, as the presentation of the checkerboards was left lateralized. Follow-up studies should involve the presentation of the stimuli in both visual fields to rule out the possibility that the observed effects are hemisphere-specific. Furthermore, it is noteworthy that this result points in a different direction from that outlined in a recent study (Zhou et al., 2021) in which modulation of the decision criterion due to expectancy induction was not reflected in a concordant modulation of the alpha amplitude. However, the experimental paradigms differ in two main aspects: a) in our study, perceptual expectations have been modulated trial-by-trial, whereas Zhou et al., (2021) have employed a block-by-block approach and b) in our design,

probabilistic contingencies were maintained continually valid, whereas in Zhou et al., (2021) they were reliable only in the first phase of each block. Thus, it can be assumed that these crucial variations in the experimental design employed explain the differential findings from the two groups.

How would voluntary regulation of pre-stimulus alpha oscillations impact the response criterion? According to the SDT framework, observers evaluate the presence vs. the absence of the stimulus by assessing whether the strength of the internal responses exceeds the decisional criterion. Any mechanism that magnifies the internal response is likely to cause exceeding the decision-making criterion. According to the Gating by Inhibition theory (Jensen and Mazaheri, 2010), alpha rhythms play a fundamental role in maintaining an active and flexible inhibition mechanism capable of modulating the excitability of the cerebral cortex. Thus, the mechanism behind the liberalization of the decisional criterion may depend on a deliberate release from inhibition by alpha desynchronization in visual regions as the probability of the target appearance increases (Foxye and Snyder, 2011). The consequent increase in neural excitability would affect not only the interpretation of signal but also noise, facilitating the internal response to exceed the decisional criterion under the same input stimulation, without actually affecting perceptual performance (Iemi et al., 2019, 2017; Samaha et al., 2020; Vugt et al., 2018).

Having highlighted that alpha amplitude in posterior regions could be regulated by voluntary top-down processes related to prior, we subsequently analysed which brain networks were engaged in this alpha rhythm tuning. Electrophysiological evidence indicates that different neuronal assemblies exchange information through phase synchronisation of oscillatory activity (Canolty et al., 2010; Fries, 2015; Varela et al., 2001). If two different brain networks oscillate in phase, they are more likely to influence each other because their excitatory state is concordant in time. Thus, we have investigated whether the long-range phase coupling along the theta and alpha bands between fronto-parietal and parieto-occipital regions come into play in the regulation of sensory oscillatory activity. The results showed that synchronization along the parieto-occipital circuit is increased in the conservative condition compared with the liberal condition along the alpha band, whereas in the fronto-parietal circuit there is an increase in theta synchrony in the liberal trials. Crucially, we isolate different influences subserved by theta and alpha synchronization on the alpha amplitude recorded in posterior regions. Interregional alpha-band phase synchronization underpins numerous cognitive processes including top-down processing, perception, attention selection, cross-modal integration and working memory (Bastos et al., 2020; Doesburg et al., 2009; Michalareas et al., 2016; van Driel et al., 2014; van Kerkoerle et al., 2014; Zanto et al., 2011). Our results expand this literature by

showing that alpha coupling is involved in the transmission of predictive-like information in human observers. Indeed, enhanced alpha synchronization in the conservative vs. liberal condition underlies a magnified prior-dependent regulation of pre-stimulus alpha amplitude. This synchronization shift may induce a modulatory effect on the levels of inhibition in the sensory cortex, making it more difficult (vs. easier) for the internal response to subsequently overcome the decision criterion. Therefore, these results point toward a crucial role of parieto-occipital interaction in exploiting perceptual expectations through controlling the level of excitation of visual areas (indicated by modulation of alpha amplitude). On the contrary, the results indicated that theta synchronization may play a diametric role in predictive processes since increased phase aligning in the liberal vs. conservative condition inhibits the prior-based differentiation of pre-stimulus alpha amplitude. Fronto-parietal theta coupling has been related to a performance monitoring system in context that require increased cognitive efficiency (López et al., 2019; Nurislamova et al., 2019). Although early studies focused on the reactive role of theta rhythm (i.e., increase after the occurrence of a cognitively challenging event), recent evidence shows that theta regulation can also be employed proactively, pre-setting the system to be sensitive to cognitively demanding events (Cooper et al., 2015) and especially when preparing to override a pre-potent response tendency (Cavanagh et al., 2013; van Noordt et al., 2017). For example, theta increase in the frontal areas act as an inhibitory control mechanism that reduce the influence of salient attribute in value-based decision making that predicts regulatory success (HajiHosseini and Hutcherson, 2021). Crucially and in agreement with what we have observed, theta oscillations are able to interplay with alpha parameters in posterior regions to implement high-level processing (Jiang et al., 2018; Min and Park, 2010; Popov et al., 2018). Thus, these results suggest that the exploitation of predictive models might be overseen by an executive mechanism traveling at slower frequencies that monitors and controls the process. Why is this dynamic required mainly in the liberal condition? The human cognitive system has an inherent bias that tends to conservative criterion placement (Rahnev and Denison, 2018) since missing the target is less detrimental than incurring frequent false alarms (Zenger and Fahle, 1997). Thus, it can be hypothesized that under conditions in which this error is more likely to emerge, a higher level of control could be required. Moreover, there is a close link between frontal functionality and false alarms (Festini and Katz, 2021) as frontal damages are associated with the establishment of a liberal response bias (Biesbroek et al., 2015).

Finally, the existence of neural mechanisms involved in the facilitation vs. attenuation of predictive processing prompted the investigation of their ability to intercept interindividual differences in prediction

handling. Specifically, individuals lie along a continuum of predictive styles at the poles of which stand the decision makers who are more inclined to use prior information vs. the observers who adopt an empirical strategy that dampens prior information in favor of sensory inputs. We have assumed that the latter (*empiricists*) would be characterized by intense use of the predictive control mechanism, placing the sensory cortex in a state of waiting for stimulation rather than prompting it in a particular state of excitability. In contrast, prior-prone individuals (*believers*) might use an intense bias mechanism in visual cortex to modulate perception in an expectation-congruent modality. Using a median split approach, we partitioned the sample according to the prior-relation alpha amplitude modulation. We demonstrated that individuals who weakly set the posterior alpha amplitude as a function of expectation showed reduced propensity to biased response coupled with an increase in fronto-parietal theta synchronization in the liberal condition. This modulation was abolished in the high alpha modulator group, which instead are characterized by a greater response bias paired with a general increase in parieto-occipital coupling in the alpha band and enhanced alpha synchronization in conservative trials compared with the liberal condition. These findings aided us in tracing the neural mechanisms potentially underlying the differences in predictive style existing in the general population. Interestingly, the two groups do not show dissimilarity in sensitivity index (d'). Hence, in the experimental context explored, both approaches succeed in ensuring adaptive behavior. Future studies should investigate whether in settings in which prior models are hyper (vs hypo) accurate (e.g., 90 vs 55% of predictive power), objective performance may diverge depending on the predictive strategy employed. Furthermore, the under-exploitation (vs. over-exploitation) of the mapped neurofunctional mechanisms could account for the behavioral failures observed in some clinical populations that are placed at maladaptive extremes of the predictive continuum (Tarasi et al., 2022). For example, reduced alpha synchronization could underlie the reduced use of prior information observed in autism (Pellicano and Burr, 2012), whereas a deficit in theta alignment could explain the lack of supervision in the utilization of priors in hallucinators (Corlett et al., 2019).

Conclusion

To sum up, the current work investigated the processes behind predictive perception showing how expectations are integrated into the human perceptual process. Results indicate that prior knowledge shapes the content of perceptual representations rather than their fidelity and that this process is enacted through a preparatory mechanism that modulates cortical oscillations, particularly in the alpha band, in perceptual regions. Inter-areas communication along the fronto-parietal-occipital pathway is crucially linked to this

strategic tuning of sensory area activity and in explaining inter-individual differences in the way prior knowledge is used. Specifically, fronto-parietal theta coupling would mediate a supervisory process of the predictive machinery (enhanced in prior-resistant individuals), whereas parieto-occipital alpha synchronization would underpin the conveyance of expectation-like information (enhanced in prior-prone individuals).

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SUPPLEMENTARY MATERIALS

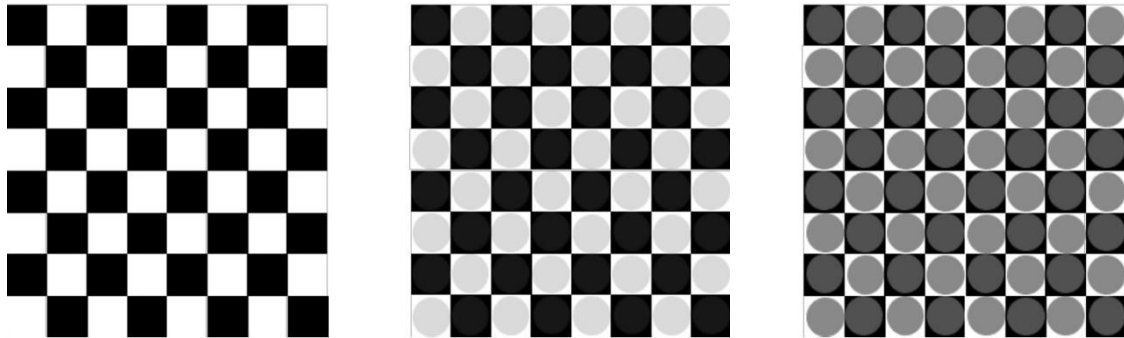
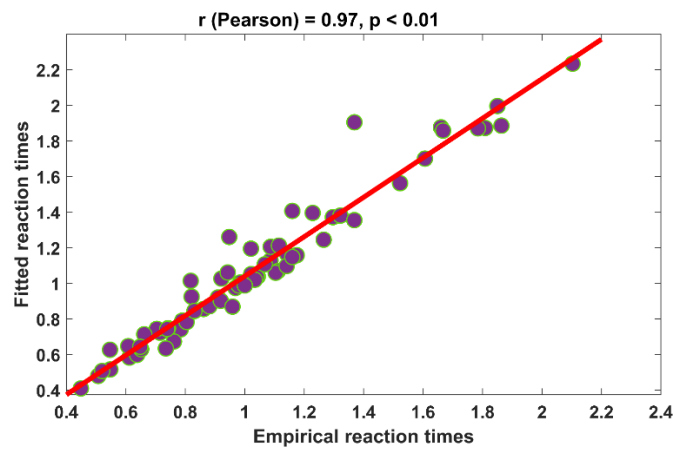
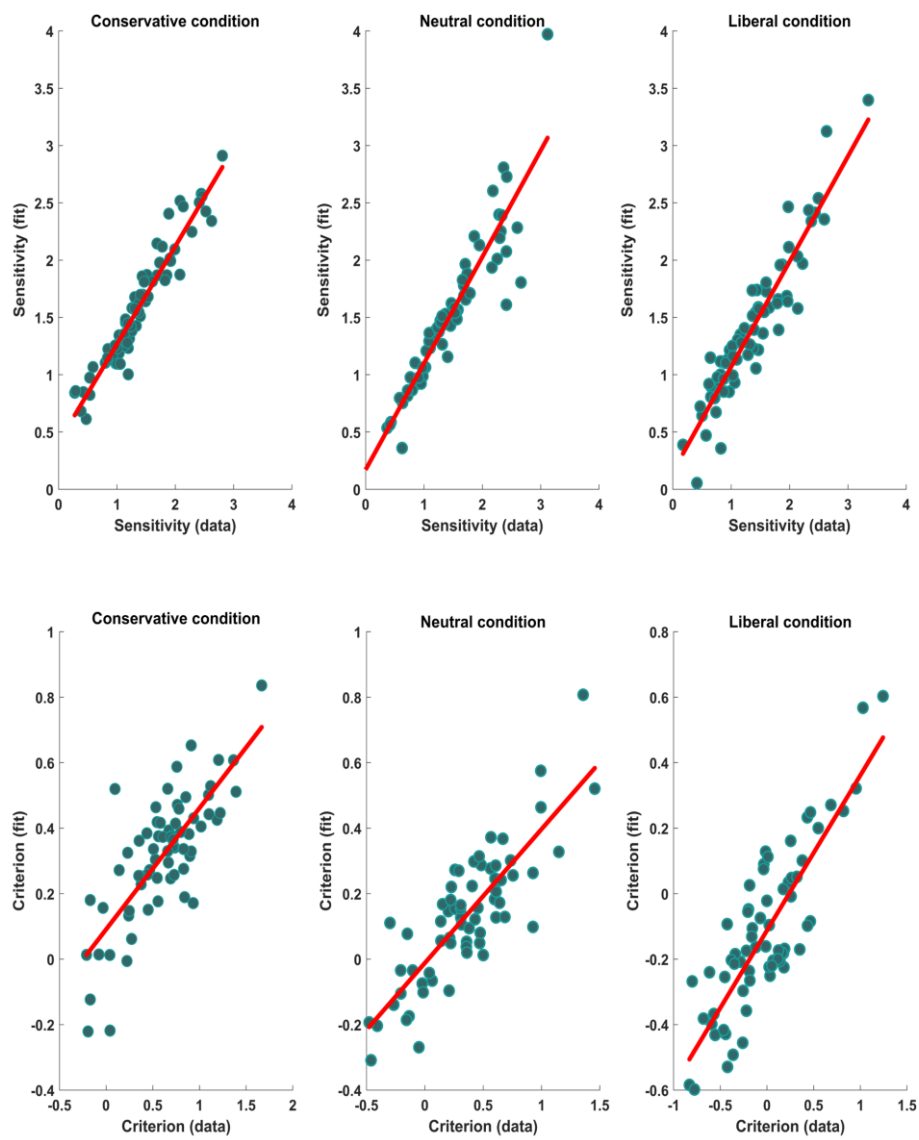


Figure S1. Examples of checkerboards presented. From left to right: Catch Stimulus, Average Contrast Stimulus (RGB contrasts: 35/223), Maximum Contrast Stimulus (RGB contrasts: 100/155).

Reaction times (seconds)	Conservative	Neutral	Liberal
Presence Choice	1.27 ± 0.56	1.12 ± 0.47	1.03 ± 0.43
Absent Choice	0.99 ± 0.38	1.04 ± 0.41	1.2 ± 0.48
Correct Choice	1 ± 0.38	1.03 ± 0.4	1.02 ± 0.4
Incorrect Choice	1.28 ± 0.61	1.2 ± 0.51	1.31 ± 0.59
Hit Rate	1.18 ± 0.5	1.09 ± 0.48	0.99 ± 0.41
False Alarm	1.51 ± 0.81	1.41 ± 0.75	1.33 ± 0.76
Correct Rejection	0.96 ± 0.36	1 ± 0.41	1.13 ± 0.46
Miss	1.19 ± 0.57	1.17 ± 0.49	1.35 ± 0.59

Table S1. Reaction Time values (seconds). There is no substantial differentiation related to condition when considering reaction times for correct vs incorrect choices. Instead, it could be observed a decrease in reaction times in congruent situations (response in the direction of prior information) and an increase in incongruent situations, testifying to the presence of a bias instillation due to the probabilistic cue.

A**B**

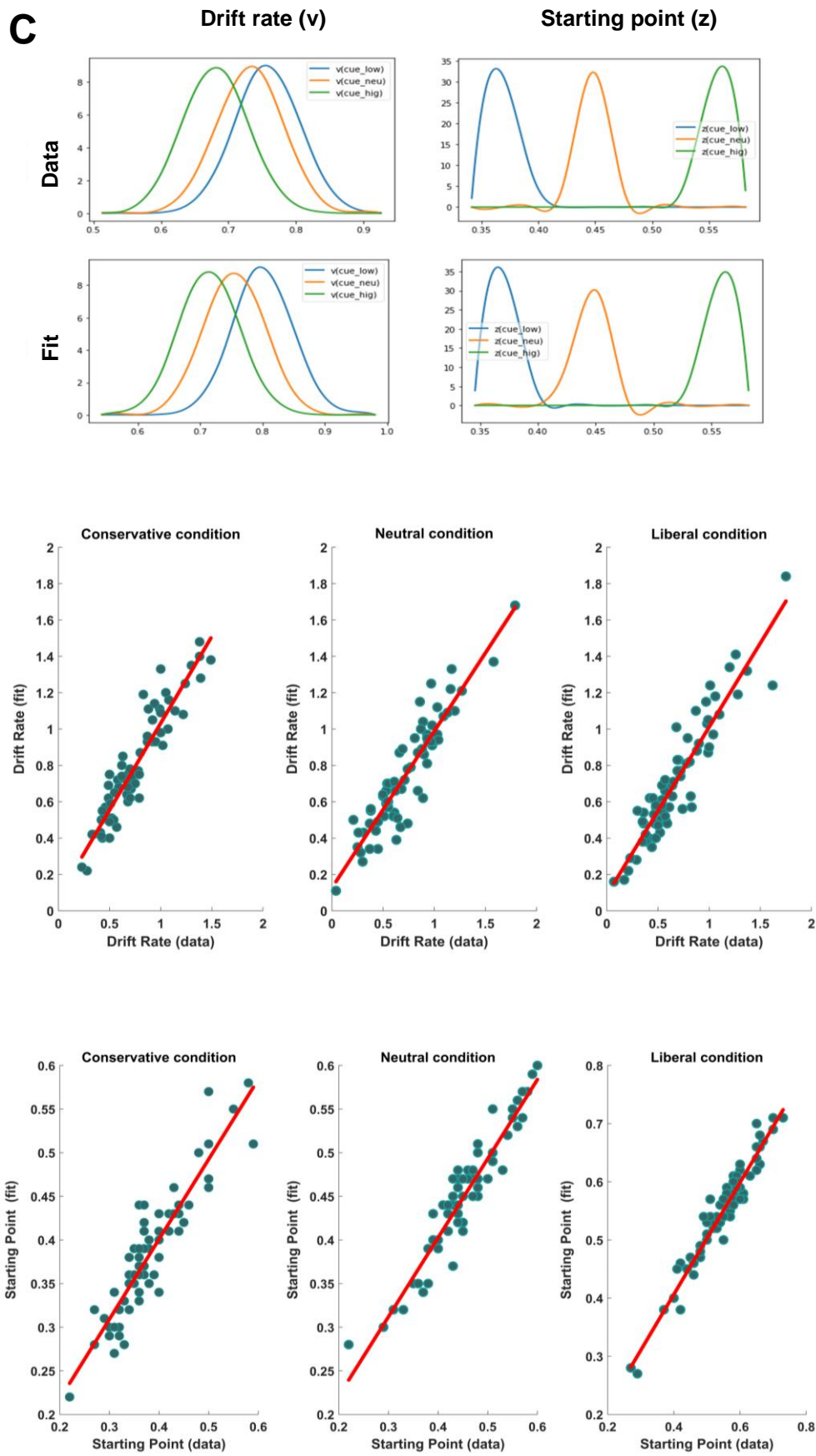


Figure S2. A. Association between actual and simulated individual reaction times considering all conditions together ($r = 0.97$; $p < 0.01$); **B.** Association between the actual sensitivity/criterion value with the sensitivity/criterion value calculated on the simulated

data, considering the three conditions separately (r value ranges between 0.77 and 0.97).

C. Posterior distribution of the parameters obtained by fitting HDDM on the real and simulated data. No significant differences between estimated and actual parameters (all $q > 0.22$) can be observed (upper panel). Actual and estimated DDM parameters significantly correlate at the individual level (r value ranges between 0.92 and 0.97; lower panel).

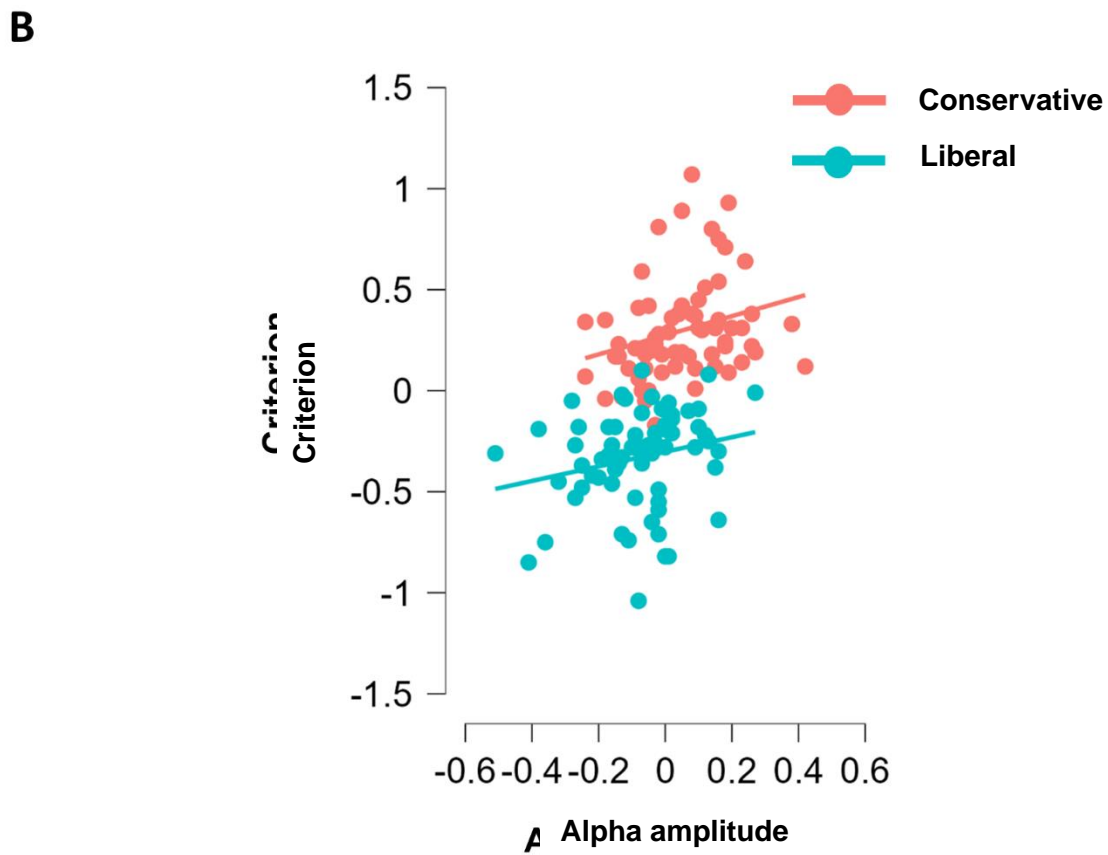
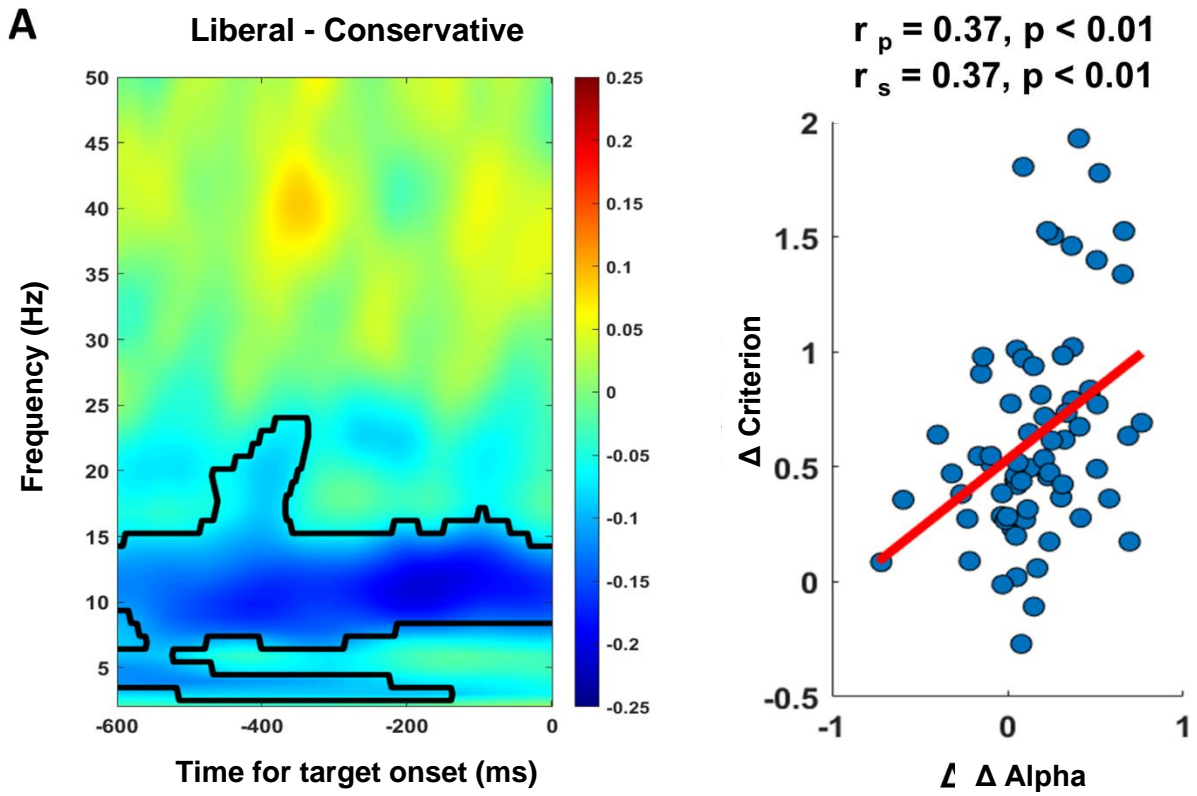


Figure S3. A. The association between behavioral and neural markers of prior information was assessed by equating the number of trials with subsampling. The pattern of results

resembles the one obtained considering the entire dataset (see Figure 4C). **B.** The linear regression analysis conducted between ALPHA AMPLITUDE and CONDITION as the independent variables and CRITERION as the dependent variable. Both ALPHA AMPLITUDE and CRITERION were normalized in order to reduce between-subject variability by subtracting, for each participant, the overall mean of the two measures from the condition-specific values. The conducted analysis demonstrated the presence of a significant effect of both ALPHA AMPLITUDE ($B = 0.47$, $t = 2.3$, $p = 0.02$) and CONDITION ($B = -0.58$, $t = -12.9$, $p < 0.01$) without any significant interaction between the two factors ($B = -0.11$, $t = -0.40$, $p = 0.69$). Therefore, the magnitude of alpha is associated with the criterion level, regardless of the specific condition. Again, the same analysis performed considering sensitivity measures (d') showed no significant relationship with the amplitude levels in either condition (all $p > 0.31$).

Signal-to-Noise Ratio (SNR) in functional connectivity analysis. Potential differences in the signal-to-noise ratio (SNR) across conditions might lead to problems in interpreting changes in connectivity as estimated with weighted phase-lag index. Crucially, in the conservative trials we have identified a larger alpha amplitude than in the liberal condition (Fig 4A, 4B; Fig S4, top-left panel). Therefore, we conducted an additional analysis to

verify whether it was merely the difference in SNR in the frequency band of interest (i.e., alpha) in the time window used for wPLI extraction (-600 – 0 ms) that was responsible for the differences in the connectivity index. For this purpose, on a subject-by-subject basis, we randomly removed the 5% of the conservative trials that showed signal amplitude in the pre-stimulus alpha band higher than the median value in this condition and the 5% of the trials that showed signal amplitude in the pre-stimulus alpha band lower than the median value in the liberal condition. Next, we calculated, in the remaining trials, the connectivity indices considering the electrode pairs (sp_sig), along the parieto-occipital circuit, found to be significantly modulated from the permutation-based analysis previously conducted (see main text). We repeated the above procedure 10 times to ensure the stability of results upon random removal of distinct trials. We then averaged the connectivity values that emerged from the 10 repetitions to obtain an average estimate per condition.

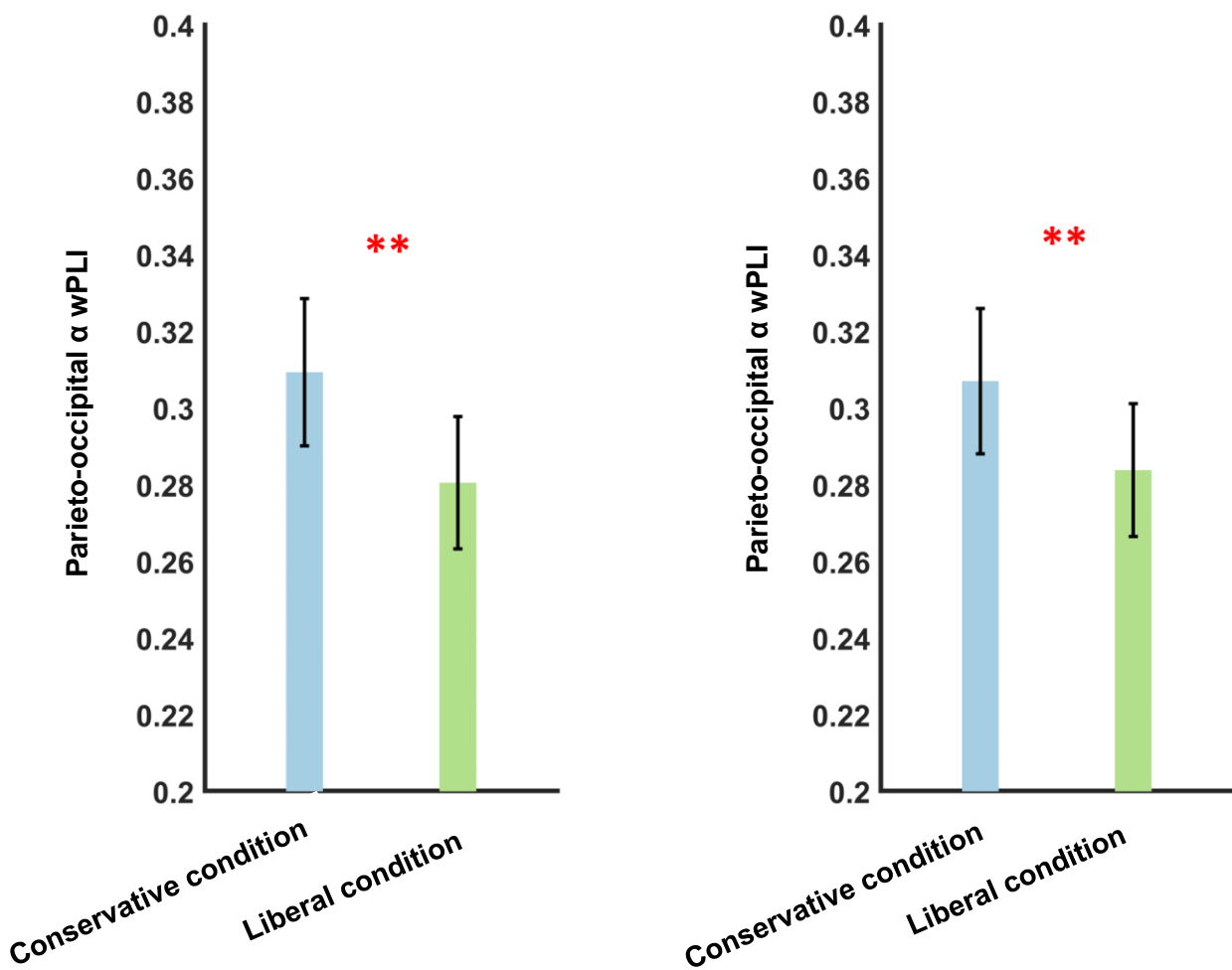
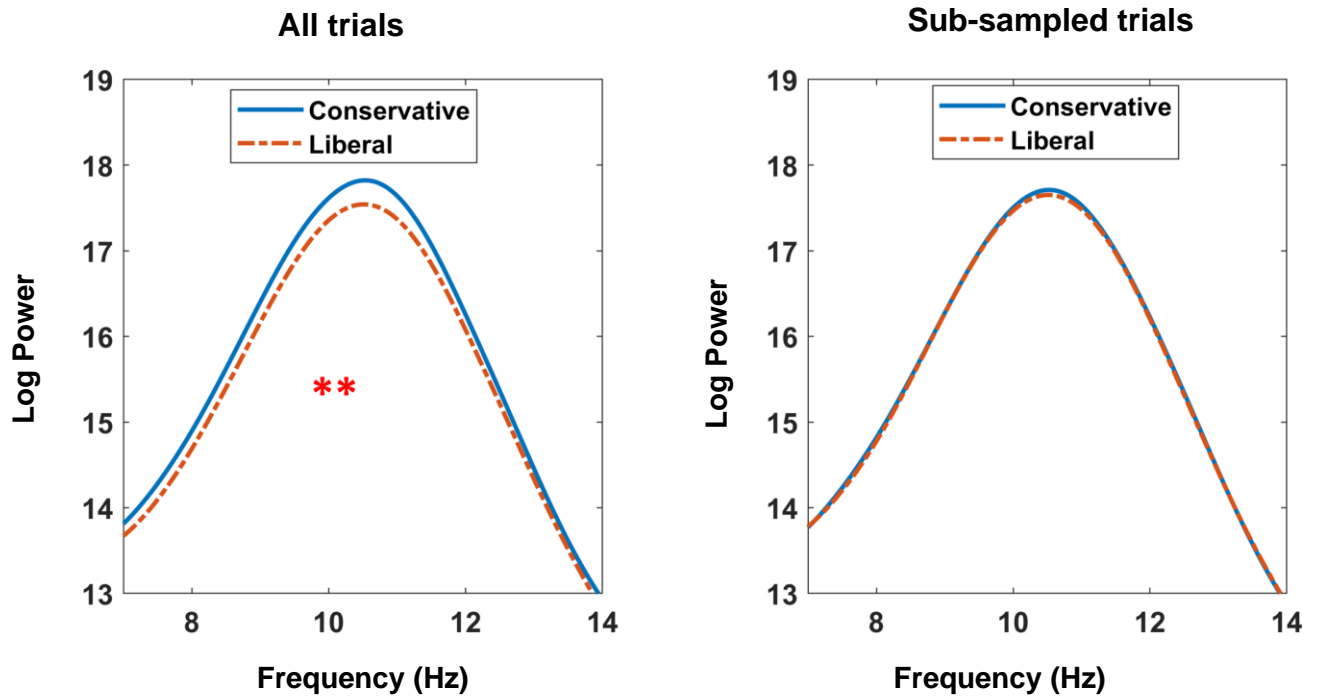


Figure S4. SNR before (top-left panel) and after (top-right panel) the subsampling procedure. A paired t-test provided statistical evidence that after subsampling procedures

there is no significant difference in SNR ($t_{67} = -0.51$, $p = 0.61$). Despite this, the increase in alpha connectivity in the parieto-occipital network in the conservative versus liberal condition as observed before subsampling (left-lower panel: $t_{67} = 3.85$, $p < 0.01$) remained statistically significant after the subsampling procedure (right-lower panel: $t_{67} = 3.22$, $p < 0.01$).

** indicates a significance level of < 0.01