

Two Oscillatory Correlates of Attention Control in the Alpha-Band with Distinct Consequences on Perceptual Gain and Metacognition

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Behavioral consequences and neural underpinnings of visuospatial attention have long been investigated. Classical studies using the Posner paradigm have found that visual perception systematically benefits from the use of a spatially informative cue pointing to the to-be-attended spatial location, compared with a noninformative cue. Lateralized α amplitude modulation during visuospatial attention shifts has been suggested to account for such perceptual gain. However, recent studies on spontaneous fluctuations of prestimulus α amplitude have challenged this notion. These studies showed that spontaneous fluctuations of prestimulus α amplitude were associated with the subjective appreciation of stimulus occurrence, while objective accuracy was instead best predicted by the frequency of α oscillations, with faster prestimulus α frequency accounting for better perceptual performance. Here, in male and female humans, by using an informative cue in anticipation of lateralized stimulus presentation, we found that the predictive cue not only modulates preparatory α amplitude but also α frequency in a retinotopic manner. Behaviorally, the cue significantly impacted subjective performance measures (metacognitive abilities [meta- d']) and objective performance gain (d'). Importantly, α amplitude directly accounted for confidence levels, with ipsilateral synchronization and contralateral desynchronization coding for high-confidence responses. Crucially, the contralateral α amplitude selectively predicted interindividual differences in metacognitive abilities (meta- d'), thus anticipating decision strategy and not perceptual sensitivity, probably via excitability modulations. Instead, higher perceptual accuracy both within and across participants (d') was associated with faster contralateral α frequency, likely by implementing higher sampling at the attended location. These findings provide critical new insights into the neural mechanisms of attention control and its perceptual consequences.

Key words: alpha amplitude; alpha frequency; attention; EEG; metacognition; visual decision making

Significance Statement

Prior knowledge serves the anticipation of sensory input to reduce sensory ambiguity. The growing interest in the neural mechanisms governing the integration of sensory input into our internal representations has highlighted a pivotal role of brain oscillations. Here we show that distinct but interacting oscillatory mechanisms are engaged during attentional deployment: one relying on α amplitude modulations and reflecting internal decision processes, associated with subjective perceptual experience and metacognitive abilities; the other relying on α frequency modulations and enabling mechanistic sampling of the sensory input at the attended location to influence objective performance. These insights are crucial for understanding how we reduce sensory ambiguity to maximize the efficiency of our conscious experience, but also in interpreting the mechanisms of atypical perceptual experiences.

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Introduction

Conscious perception has become the object of many scientific investigations, and influential theories have proposed that it arises from the recurrent interaction between sensory input and internal predictive representations (Lamme and Roelfsema, 2000; Engel et al., 2001; Friston, 2009, 2010, 2019). Yet, how sensory input and top-down control interact to give rise to our conscious perceptual experience remains largely unknown.

A number of studies have pointed to an active role of prestimulus α oscillations in sensory processing. They highlighted an inverse link between posterior α amplitude and excitability of visual areas (Romei et al., 2008a, b), with reduced α amplitude predicting improved perceptual performance (Ergenoglu et al., 2004; Hanslmayr et al., 2007; van Dijk et al., 2008). This initial interpretation has been refined though, with new evidence suggesting that α amplitude covaries with the internal predisposition toward perceptual experience leading to more conservative versus liberal attitudes (low/high confidence in perception associated with low/high cortical excitability and higher/lower α amplitude) (Limbach and Corballis, 2016; Benwell et al., 2017, 2022; Samaha et al., 2017; Iemi and Busch, 2018; Iemi et al., 2019; Di Gregorio et al., 2022b). A possible mechanistic explanation is that modulation of α amplitude and hence excitability affects not only the interpretation of signal but also noise, hence leading to sensory bias (Samaha et al., 2020). Moreover, recent evidence from our group shows that α amplitude not only accounts for perceptual confidence (Di Gregorio et al., 2022b); indeed, we found that poststimulus α amplitude predicts subjective metacognitive performance, an index reflecting the efficacy of confidence ratings to discriminate correct from erroneous responses in perceptual tasks, thus suggesting a role of poststimulus α amplitude in integrating sensory input into the internal representation (Di Gregorio et al., 2022b).

What are then the neurophysiological underpinnings of objective performance? Recent studies (Cecere et al., 2015; Samaha and Postle, 2015; Mierau et al., 2017; Wutz et al., 2018; Zhang et al., 2019) point to a role of α frequency in perceptual sampling, with faster frequency leading to higher sensory resolution. In line with this literature, Di Gregorio et al. (2022b), using rhythmic TMS (as in Romei et al., 2016), showed that speeding up/slowing down individual prestimulus α frequency (but not α amplitude) by TMS enhances/impairs task accuracy. These results suggest that the speed of one α cycle influences processing efficiency, thus dictating the level of perceptual sensitivity, with more effective sensory sampling per cycle for higher than lower α frequencies (Trajkovic et al., 2021; Coldea et al., 2022; Di Gregorio et al., 2022b).

In sum, there is a growing consensus about the dissociable roles of α frequency and amplitude in shaping sensory input and its subjective interpretation. However, it is hard to imagine that these two mechanisms are not comodulated and also interact to optimize the efficiency of our perceptual experience. Attention is certainly one of the key mechanisms that may lead to a comodulation of these processes, whereby the limited resources, in terms of both shaping sensory sampling and sensory bias, are expected to be directed toward the to-be-attended spatial location, thus ensuring maximum perceptual efficiency where the relevant stimulus is expected. Therefore, we predicted that attention deployment leads to a comodulation of the circuits of sensory bias (i.e., α amplitude) and sensory precision (i.e., α frequency).

The current study aimed to test these predictions, via manipulation of spatial attention before stimulus onset. Specifically, we presented an attentional cue informing with high validity (75%)

upcoming lateralized stimulus location. In line with many previous reports (e.g., Sauseng et al., 2005; Thut et al., 2006), we expected attentional cueing to modulate both prestimulus α amplitude lateralization and perceptual performance. Importantly, we hypothesized that, despite their co-occurrence, α amplitude would not directly account for changes in objective but rather for subjective perceptual performance. More specifically, depending on the extent to which our confidence in our subjective experience is consistent with our probability of being correct, also called metacognition, and which reflects the extent to which objective and subjective processes align (Di Luzzio et al., 2022), we expected α amplitude changes with attention to account for changes in metacognitive abilities and this already during the prestimulus period, as induced by the predictive cue. We, however, did not expect changes in α amplitude to predict objective performance (d'). Conversely, we expected this objective perceptual performance measure to be enhanced by the allocation of sensory sampling resources at the to-be-attended location (i.e., via faster α -frequencies).

Materials and Methods

Participants

Twenty-four healthy volunteers (12 women; mean age = 23.2 years, SE = 2.61 years) were recruited for the study, at the Center for Studies and Research in Cognitive Neuroscience in Cesena, Italy. The same participants also took part in a second study, reported previously (Di Gregorio et al., 2022b), and involving different task conditions where the informative cue was not present (Di Gregorio et al., 2022b, their Experiment 1; Trajkovic et al., 2022). The study was approved beforehand by the bioethics committee of the University of Bologna, and all participants gave written informed consent to participate in the study.

Stimuli and procedure

The Experimental task was controlled via the E-Prime software (Psychology Software Tools), and stimuli were presented on a CRT monitor (100 Hz refresh rate, 57 cm viewing distance). Each trial of the task involved a primary response on the visual detection task of the perithreshold target stimuli, and a secondary rating of confidence, in which participants rated the level of confidence on their accuracy on a scale 1-4 (1 = no confidence at all; 2 = little confidence; 3 = moderate confidence; 4 = high confidence). Each trial began with a white fixation cross on the center of the screen (duration = 2000 ms; visual angle = 0.8°). Afterward, an informative cue appeared to indicate the spatial position of the following primary task stimulus. The cue was a white arrow (duration = 2000-3000 ms, visual angle = 2°) presented in the center of the screen, which could point either to the left or to the right part of the visual field. In 75% of cued trials, the cue correctly predicted the position of the primary task stimulus (valid cue condition); and in the remaining 25% of trials, the cue pointed in the other direction (invalid cue condition).

The two possible cues (valid and invalid cue) were immediately followed by the primary task stimulus (duration = 60 ms, 4.1°/3.7° eccentricity in the lower part of left or right visual field), that could be either a catch stimulus or a target stimulus. Stimuli used were the same as in Di Gregorio et al. (2022b): 8 × 8 black-and-white checkerboards (height = 4 cm; width = 4 cm, visual angle = 15.9°) that could (target stimuli) or not (catch stimuli) contain iso-luminant gray circles (for details, see Di Gregorio et al., 2022b). Whenever the participants perceived the circles embedded within the checkerboard stimulus, they were prompted to press the spacebar on the keyboard (Fig. 1).

Titration session

Before the main experimental session, in a titration session, perithreshold intensity of the iso-luminant circles was identified for every participant (for details, see Di Gregorio et al., 2022b). In sum, 8 different contrast ratios (RGB contrasts on black/white background: 28/227, 32/223, 36/219, 40/215, 44/211, 48/207, and 100/155) were presented along with catch trials (checkerboards without iso-luminant circles), and the

obtained data were used for the sigmoid fitting, whereby the inflection point was considered as the individual threshold value of the target stimulus. These threshold values were subsequently used to individually tailor the stimuli of the main experimental task. For all participants, the luminance contrast ratio was selected in a range between 20/235 and 50/205 RGB points (mean = 32/223; SE = 12).

Main experiment

Although response speed for visual detection was never stressed in favor of perceptual accuracy, a time limit of 2000 ms was given. Immediately after the primary task response, a confidence prompt appeared on the screen with the Italian version of the question: “How confident are you about your response?” Confidence rating consisted of a 4 point Likert scale ranging from “no confidence at all” to “high confidence.” After the secondary confidence rating, a new trial started (total trial number = 300).

EEG data

Psychophysiological recording. EEG data were collected from 64 Ag/AgCl electrodes (Brain Products). Electrodes were placed according to the 10:10 international system. Two additional electrodes served as the reference (placed on the left mastoid) and the ground (placed on the right cheek). The electro-oculogram (EOG) was recorded from above and below the left eye and from the outer canthi of both eyes. EEG and EOG were recorded with a bandpass filter of 0.01–100 Hz at a sampling rate of 1000 Hz, which was resampled to 500 Hz offline. The impedance of all electrodes was kept to <10 k Ω .

EEG data were preprocessed using custom-made routines in MATLAB R2013b (The MathWorks). First, EEG data were rereferenced offline to the average of all electrodes and filtered with a 0.5–30 Hz passband. Stimulus-locked epochs were then extracted, from -2000 to 2000 ms with a baseline set from -2000 to -1500 ms. Epochs containing artifacts were excluded via a twofold procedure: first, the `pop_autorej` function in EEGLAB version 13.0.1 (Delorme and Makeig, 2004) was used to exclude trials with high voltage fluctuations (>1000 μ V) or containing data values outside an interval of 5 SDs. Additionally, we specifically controlled for ocular artifacts by applying artifact rejection on epochs with outlier values over horizontal and vertical EOG (percentage of excluded trials: 6.04%, SE = 0.51%). After artifact rejection, the function `lms_regression` for automatic EOG correction using Least Mean Squares was applied (`lms_regression` function in MATLAB R2013b) (Gratton et al., 1983). Because α suppression is larger contralaterally to cue direction, we compared activities from contralateral and ipsilateral electrodes for the analyses. To this aim, data epochs for right-cued stimuli were copied and flipped to the right side of the original data, resulting in conventionally defined right hemisphere activity as contralateral, and left-hemisphere activity as ipsilateral, to cue direction (Di Gregorio et al., 2022b).

Invalid cue data, representing a residual 25% of trials where the cue incorrectly indicated the position of the forthcoming stimulus ($N = 75$), were not considered in the analyses.

Alpha frequency. Individual α frequency peak during the task was calculated in the cue-stimulus period (i.e., prestimulus α from -1000 ms to stimulus presentations), by implementing a fast Fourier transformation (MATLAB function `spectopo`, frequency resolution: 0.166 Hz). Preliminary analyses were performed to investigate the effects of the presentation of a visuo-spatial cue over the hemispheric distribution of α frequency. Then, analyses were performed separately for each subject and condition to investigate the relation between α frequency and perceptual performance. Alpha frequency was defined as the local maximum power within the frequency

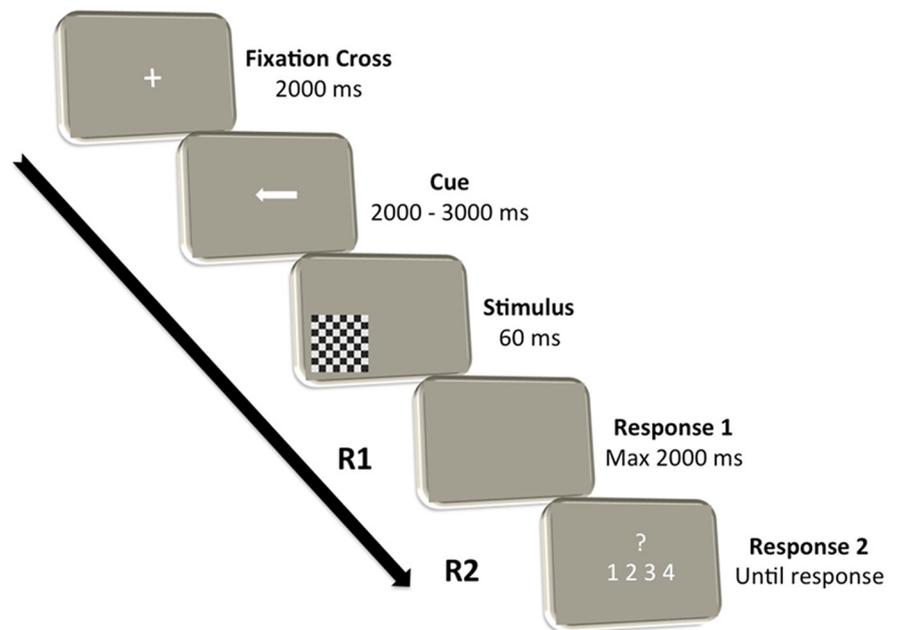


Figure 1. Trial sequence. Each trial started with a fixation cross; then a cue indicates (left or right arrow, valid cue: 75% predictivity) the probability of the position of the forthcoming stimulus (a checkerboard). The primary task was to respond (R1) if the checkerboard contained gray circles. After this primary response, participants rated their confidence (R2) in their first response on a Likert scale from 1 (no confidence at all) to 4 (high confidence). ms, milliseconds.

range of 7–13 Hz (i.e., α peak). The following subset of posterior parieto-occipital electrodes was used: contralateral electrodes (P8, P6, P4, P2, PO8, PO4, O2), ipsilateral electrodes (P7, P5, P3, P1, PO7, PO3, O1). Although each participant showed a clear peak within this range with maxima over these posterior electrodes, peak electrodes varied across participants. For this reason, we visually inspected power spectra on the posterior electrodes, and chose for each participant a contralateral electrode with a clear peak of the maximum power (Samaha and Postle, 2015; Di Gregorio et al., 2022b). The homologous electrode was selected for the analyses in the ipsilateral hemisphere.

Alpha amplitude. Spectral EEG activity was assessed by time frequency decomposition using a complex sinusoidal wavelet convolution procedure (between 2 and 25 cycles per wavelet, linearly increasing across 50 linear-spaced frequencies from 2.0 to 50.0 Hz) with the `newtimef` function in EEGLAB version 13.0.1 (Delorme and Makeig, 2004) and custom routines in MATLAB. Preliminary analyses on α amplitude were performed in a large cue-locked time window (-700 ms to stimulus presentation) to investigate the effects of the visuo-spatial cue on the hemispheric distribution of α amplitude. Then, prestimulus analyses were performed. To this aim, single-trial baseline between -2000 and -1500 ms preceding stimulus onset was used. The resulting power was normalized by decibel ($\text{dB} = 10 \cdot \log_{10}[\text{power}/\text{baseline}]$). This procedure was applied separately for each subject and condition to investigate the relation between α amplitude and perceptual performance. The same method and subsets of posterior contralateral and ipsilateral electrodes used for α frequency were used for α amplitude analyses, whereby, for each participant, the contralateral electrode with maximum α suppression was selected, along with its ipsilateral homolog. Therefore, the most negative value (i.e., α amplitude) in the α range (7–13 Hz) was identified separately for each condition in the cue-stimulus time period (from -400 ms to stimulus presentation) (Samaha et al., 2017). Finally, α amplitude was normalized by subtracting from each electrode used in the analyses the mean of the alpha power over the entire posterior parieto-occipital electrode cluster.

Behavioral measures

Data were sorted according to the cue information (valid vs invalid cue). d' was computed on this dataset and directly compared with the d' dataset computed in Di Gregorio et al. (2022b), on the same group of participants involved in the same task during the presentation of an

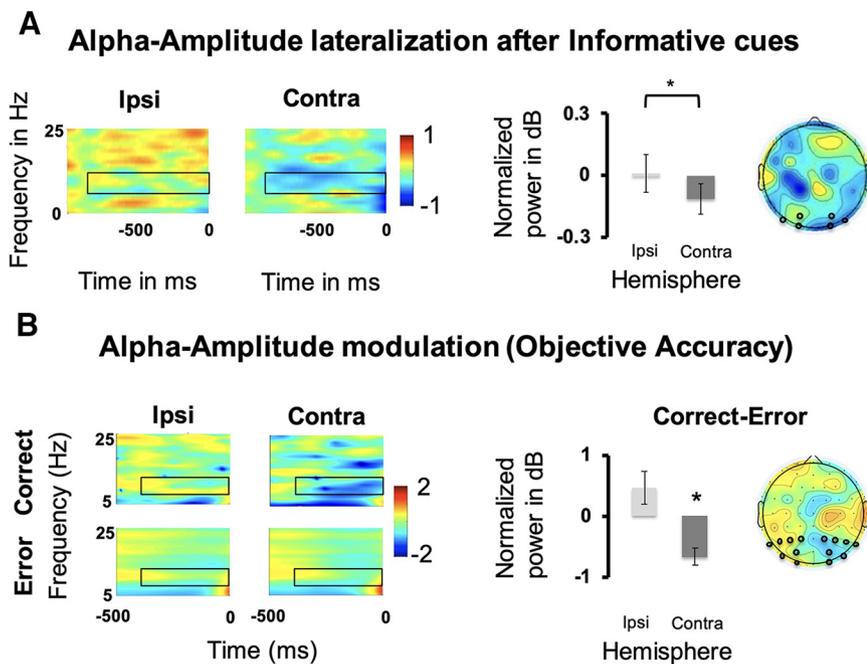


Figure 2. *A*, Prestimulus cue-locked α amplitude in the ipsilateral and contralateral hemispheres is reported in the cue-stimulus time period after informative cues as time frequency plots. Data are reported from the maxima α suppression in the ipsilateral and contralateral hemisphere. Black boxes represent regions of statistical analyses (alpha band 7–13 Hz, time window: -700 ms to stimulus presentation). Bar graph is reported for normalized power in the ipsilateral and contralateral hemispheres. Topography represents the α amplitude distribution over electrodes (electrodes are flipped to have contralateral activity in the right-hand side and ipsilateral activity in the left-hand side). Black circles represent selected electrodes. *B*, Prestimulus α amplitude in the ipsilateral and contralateral hemispheres is reported in the cue-stimulus time period for correct and error trials. Data are reported from the electrodes with the maxima α suppression in the ipsilateral and contralateral hemisphere. Black boxes represent regions of statistical analyses (alpha band 7–13 Hz, time window: 400 ms to stimulus presentation). Bar graph is reported for normalized power in the ipsilateral and contralateral hemispheres for the difference Correct – Error. Topography represents the difference between correct and error trials (electrodes are flipped to represent contralateral activity in the right-hand side and ipsilateral activity in the left-hand side). Black circles indicate individual selected electrodes for each participant. $*p < 0.05$ (two-tailed t test). Error bars indicate SEM. Diff, Difference. Hz, Hertz; ms, milliseconds; dB, decibel.

uninformative (neutral) cue. A direct t test for d' in the informative versus uninformative cue conditions was performed to test for the behavioral advantage induced by the informative relative to the uninformative cue condition. Moreover, all trials were sorted according to the primary task response in correct (correctly detected target and catch trials) and error trials (misses after target trials and false alarms [FAs] after catch trials). Then, in a second step, we focused on confidence level after correct trials (i.e., subjective confidence). In order to contrast confident versus nonconfident responses, correct trials were divided in high confident (i.e., confidence rating 3 and 4) and low confident (i.e., confidence rating 1 and 2).

d' . Perceptual sensitivity was estimated on the accuracy data using the d' measure, considered an unbiased measure of discrimination abilities between the signal and noise in the Signal Detection Theory (SDT) (Green and Swets, 1966). d' was calculated as $d' = z(H) - z(FA)$, where z represents the z scores of Hit rate (i.e., H), the probability of correct reactions on target trials) and FAs (i.e., the probability of incorrect reactions on catch trials) (Green and Swets, 1966).

Meta- d' . Metacognitive performance was quantified using the computational method proposed by Maniscalco and Lau (2012). Here, metacognitive accuracy is defined as the efficacy of confidence ratings to discriminate between correct and erroneous responses in an SDT model (Type II sensitivity). Briefly, the central idea is to link Type I and Type II SDT models to compute the observed Type II sensitivity. *Meta- d'* estimates the values, which maximize the fit between the observed Type II data and the parameter values of the d' Type I SDT model. Here, *meta- d'* was calculated with the function `fit_meta_d_SSE` in MATLAB. This function minimizes the sum of squared errors and estimates *meta- d'*

using observed Type II data and the empirical Type I criterion $c' > 90$. In this way, *meta- d'* estimates, for instance, the relative likelihood to report a high confidence rating after a correct response. Higher values of *meta- d'* correspond to participants having better metacognitive abilities.

Statistical analyses

Behavioral analyses. Behavioral analyses were performed separately for objective accuracy and subjective confidence, and performance in the neutral, uninformative condition (see Di Gregorio et al., 2022b) versus informative (valid cue) condition was compared.

Within-participants EEG analysis. As already reported in the literature (Kelly et al., 2006; Thut et al., 2006; Jensen and Mazaheri, 2010; Klimesch, 2012), the presentation of an informative cue induces an interhemispheric imbalance of α amplitude with larger α desynchronization contralateral to the attended location. Thus, in a first step of analysis, we aimed to replicate this finding by comparing α amplitude in the ipsilateral versus contralateral cued location. For this analysis, both valid and invalid cue conditions were merged to specifically study the effect of the cue over interhemispheric α distribution.

Then, for Objective Accuracy, we compared alpha activity (both frequency and amplitude) in a 2×2 repeated-measures ANOVAs with the factors ACCURACY (correct trials = 258.8, SE = 4.39; error trials = 23.04, SE = 3.64) and HEMISPHERE (contralateral and ipsilateral).

For Subjective Confidence, analyses were performed on correct trials (Yeung and Summerfield, 2012). Alpha activity (both amplitude and frequency) was calculated for the factor CONFIDENCE (high confidence trials = 229.7, SE = 9.26, low confidence trials = 26.5, SE = 5.42) and for the factor HEMISPHERES (contralateral and ipsilateral) in a 2×2 repeated-measures ANOVA.

In order to affirm whether trial number influences results of within-participants' EEG analyses, a trial number-matching procedure between correct and error trials was applied (accuracy analysis) and between high and low confidence trials (confidence analysis). Within this procedure, for each participant, the condition with the smaller trial number was identified (trial number = N-inferior), separately for accuracy and confidence. Then, the same number of trials in the other condition (N-superior) was randomly selected. The randomization was repeated N-inferior times and corresponding EEG data from the N-superior condition were selected and averaged. Finally, EEG data were compared between N-inferior and N-superior conditions.

For all analyses, violations of sphericity were accounted for via Greenhouse-Geisser corrections, whenever appropriate (Greenhouse and Geisser, 1959). Differences between conditions were tested by two-tailed t test planned comparisons.

Correlational analysis. Between-participant EEG analyses were related to perceptual sensitivity and metacognitive performance, based on the within-participant results. For perceptual sensitivity analyses, we looked at the relationship between the d' scores and α frequency in the contralateral and ipsilateral hemisphere, by using nonparametric robust correlation estimates (skipped Spearman correlations). The advantage of this correlation approach is that it takes into account the presence of bivariate outliers (by excluding them), and thus is not sensitive to the presence of extreme values in the overall structure of the data (Pernet et al., 2013). Similarly, we looked at the relationship between both ipsilateral

and contralateral modulations of α amplitude and meta- d' scores by using the same correlation estimates.

As a control analysis, we also looked at relations between α amplitude and d' , as well as α frequency and meta- d' , where no significant correlations were expected.

Results

Replicating previous findings: informative spatial attention cues modulate prestimulus α amplitude lateralization and enhance perceptual performance

The presentation of informative visuo-spatial attention cues instructing the allocation of spatial attention to one of the two visual fields has often been associated with a hemispheric asymmetry of α amplitude (Kelly et al., 2006; Thut et al., 2006; Rihs et al., 2007; Jensen and Mazaheri, 2010; Foxe and Snyder, 2011; Klimesch, 2012). First, we here replicate this robust finding, thus observing that an informative cue systematically induces a differential modulation of α amplitude across the hemispheres, with significantly higher α amplitude ipsilateral versus contralateral to cued location ($t_{(23)} = 2.09$, $p = 0.047$; $d = 0.43$; Fig. 2A). In addition, by directly comparing the behavioral performance for the informative versus a neutral cue condition (collected in the same participants but analyzed in terms of EEG signatures elsewhere, see Di Gregorio et al., 2022b), we found that d' values were significantly enhanced for presentation of a valid cue ($d' = 3.16$, $SE = 0.16$) compared with an uninformative (neutral) cue ($d' = 2.02$, $SE = 0.13$) ($t_{(23)} = 6.34$; $p < 0.001$; $d = 1.28$, Di Gregorio et al., 2022b). For the behavioral results of the perceptual task, see Table 1.

Moreover, previous findings consistently showed that this predictive spatial information enhances perceptual performance at the attended location through α amplitude modulation. In line with this view, when analyzing α amplitude as a function of trial accuracy (correct, incorrect) and hemisphere (contralateral, ipsilateral to attention), we observed a significant ACCURACY \times HEMISPHERE interaction ($F_{(1,23)} = 11.43$; $p = 0.003$; $\eta_p^2 = 0.332$). In particular, for correct compared with erroneous responses, we observed a suppression of prestimulus α amplitude in the contralateral hemisphere ($t_{(23)} = 2.27$; $p = 0.033$; $d = 0.45$) and a marginally significant synchronization in the ipsilateral hemisphere ($t_{(23)} = 2.01$, $p = 0.056$; $d = 0.41$) (Fig. 2B). The same analyses on accuracy effects were also performed in the averaged contralateral versus ipsilateral parieto-occipital clusters. However, the results did not show the interaction ACCURACY \times HEMISPHERE ($F_{(1,23)} = 0.374$; $p = 0.547$; $\eta_p^2 = 0.016$).

The impact of informative cue on prestimulus α amplitude lateralization shapes metacognition, not performance per se

Therefore, in line with the previous literature, we here show that the informative cue modulates prestimulus α lateralization such that contralateral (vs ipsilateral) α amplitude to the attended visual field is reduced, and that this asymmetry relates to perceptual performance (Fig. 2).

These findings can be interpreted in two ways. The traditional and most straightforward interpretation is that these two measures are directly related and more specifically that α amplitude lateralization may drive the perceptual performance improvement. However, it is also conceivable that α amplitude only coincides with, as opposed to directly influences, perceptual performance (with performance being driven by another attention-related process). Instead, α amplitude may drive subjective visual performance, such as confidence in the percept and meta- d' , an index

Table 1. Behavioral results^a

	Target	
	Present	Absent
Response	44.53% (1.1%)	2.64% (0.68%)
No response	5.59% (1.01%)	47.22% (0.72%)

^aPercentages of trials [mean (SE)] for hits, FAs, misses, and correct rejections.

accounting for the level of the individual metacognitive ability, as recent findings from our (and other) laboratories have suggested (e.g., Di Gregorio et al., 2022a, b; see Introduction). Here, we directly tested the hypothesis that the cue-related change in α amplitude for valid trials specifically impacts on metacognitive abilities, rather than perceptual sensitivity.

First, similar to the d' values, we found that metacognitive performance, measured via meta- d' scores, is significantly higher when the informative valid cue is presented (meta- $d' = 3.16$, $SE = 0.16$), compared with an uninformative (neutral) cue (neutral cue, meta- $d' = 1.98$, $SE = 0.20$) ($t_{(23)} = 5.08$; $p < 0.001$; $d = 1.04$) (Di Gregorio et al., 2022b), thus speaking in favor of the positive impact of the attentional focus on metacognitive abilities of the participant.

Second, in line with recent findings (Di Gregorio et al., 2022b), we found that prestimulus α amplitude can account for an internal predisposition toward perceptual experience (confidence levels), as suggested by a significant CONFIDENCE \times HEMISPHERE interaction ($F_{(1,21)} = 19.66$; $p < 0.001$; $\eta_p^2 = 0.484$). Specifically, high relative to low confident trials were best accounted for not only by an overall α suppression, as in our previous study where attention was not manipulated (Di Gregorio et al., 2022b); rather, they preceded by a selective α desynchronization contralateral to the attended hemifield ($t_{(21)} = 2.56$; $p = 0.018$; $d = 0.54$) along with a significantly higher ipsilateral synchronization ($t_{(21)} = 2.44$; $p = 0.023$; $d = 0.52$) (Fig. 3A). For high confident trials, this resulted in a significant difference between contralateral suppression and ipsilateral synchronization ($t_{(21)} = 2.56$; $p = 0.018$; $d = 0.54$). Moreover, an opposite pattern was observed for low confident trials (more synchronized activity contralateral and more suppressed activity ipsilateral to the cued location; $t_{(21)} = 2.38$; $p = 0.027$; $d = 0.51$). The same analyses on confidence effects were also performed in the averaged contralateral versus ipsilateral parieto-occipital clusters. Results confirmed our findings showing larger α amplitude suppression for high confidence (normalized power = -0.369 db, $SE = 0.145$ db) relative to low confidence trials (normalized power = 0.167 db, $SE = 0.141$ db) in the contralateral hemisphere ($t_{(21)} = 2.088$, $p = 0.049$, $d = 0.445$) and larger suppression in the contralateral relative to the ipsilateral hemisphere (normalized power = -0.046 db, $SE = 0.107$ db) for high confidence trials ($t_{(21)} = 2.302$, $p = 0.032$, $d = 0.491$). This was confirmed by trial matching analyses also showing larger α amplitude suppression for high confidence (normalized power = -1.433 db, $SE = 0.323$ db) relative to low confidence trials (normalized power = 0.564 db, $SE = 0.292$ db) in the contralateral hemisphere ($t_{(21)} = 4.112$, $p < 0.001$, $d = 0.839$). These findings suggest that, in addition to the contralateral α desynchronization, an ipsilateral inhibitory process is implemented, able to steer confidence resources away from the to-be-ignored spatial location and toward the cued spatial location, in high confidence trials.

Third, and in line with our hypothesis, our findings show that the effect of the informative cue on α amplitude modulations can account for individual metacognitive abilities already before stimulus presentation. Indeed, interindividual differences in the

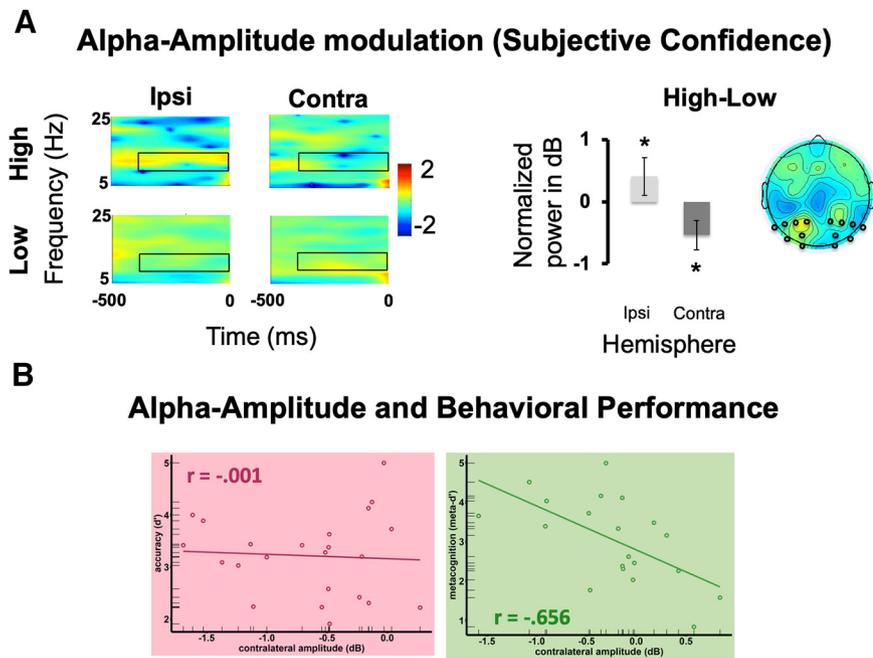


Figure 3. **A**, Prestimulus α amplitude in the ipsilateral and contralateral hemispheres is reported in the cue-stimulus time period for High and Low confidence trials. Data are reported from the electrodes with the maxima α amplitude suppression in the ipsilateral and contralateral hemisphere. Black boxes represent regions of statistical analyses (alpha band 7–13 Hz, time window: 400 ms to stimulus presentation). Bar graph is reported for normalized power in the ipsilateral and contralateral hemispheres for the difference High – Low. Topography represents the difference between High and Low confidence trials (electrodes are flipped to represent contralateral activity in the right-hand side and ipsilateral activity in the left-hand side). Black circles indicate individual selected electrodes for each participant (**B**). Correlation between α amplitude and behavioral performance for accuracy (d' measure) and metacognition (meta- d' measure). * $p < 0.05$ (two-tailed t test). Error bars indicate SEM. Diff, Difference; Hz, Hertz; ms, milliseconds; dB, decibel.

contralateral prestimulus α amplitude were able to explain differences in metacognitive abilities. Specifically, the higher the desynchronization of the α amplitude in the contralateral hemisphere, the higher the metacognitive abilities of the participant as measured via meta- d' score ($r = -0.656$, CI = $[-0.859, -0.306]$, Fig. 3B). On the other hand, ipsilateral modulations of α amplitude could not account for interindividual differences in meta- d' ($r = -0.019$, CI = $[-0.560, 0.253]$), speaking in favor of the crucial role of the contralateral hemisphere in shaping metacognitive abilities across participants, as also previously reported (Di Gregorio et al., 2022b). Finally, in line with recent findings, our results confirm that neither contralateral nor ipsilateral modulations of α amplitude could directly account for modulations in perceptual accuracy as measured with d' (contralateral: $r = -0.001$, CI = $[-0.532, 0.470]$, Fig. 3B; ipsilateral: $r = 0.261$, CI = $[-0.203, 0.640]$).

Together, these findings suggest that, away from the classical interpretation, contralateral modulations of α amplitude following informative cue presentation predict confidence, directly impacting on metacognitive abilities and not on perceptual sensitivity per se.

The impact of informative cue (for valid trials) on contralateral prestimulus α frequency shapes perceptual sensitivity, not metacognitive abilities

According to Di Gregorio et al. (2022b), a better candidate to account for changes in perceptual sensitivity is the frequency and not the amplitude of posterior α oscillations (for a similar account, see also Coldea et al., 2022). Specifically, considering the impact that the informative cue has on perceptual performance at the

attended location, being significantly improved, one may expect this effect to be determined by a speeding up of α frequency specifically at posterior brain areas contralateral to the attended location.

Indeed, the informative cue induced an interhemispheric modulation of α frequency, with significantly faster α contralateral versus ipsilateral to cued location ($t_{(23)} = 2.55$; $p = 0.018$; $d = 0.52$) (Fig. 4A).

Furthermore, our results showed that α frequency was able to distinguish between correct and erroneous responses, as we found a main effect of ACCURACY for α frequency ($F_{(1,23)} = 4.68$; $p = 0.041$; $\eta_p^2 = 0.169$), as well as a significant ACCURACY \times HEMISPHERE interaction ($F_{(1,23)} = 6.63$; $p = 0.017$; $\eta_p^2 = 0.224$), pointing to a lateralized relationship of α frequency with accuracy. Specifically, in line with our hypothesis, a speeding-up of α frequency could be observed selectively in the hemisphere contralateral to the attended hemifield for correct responses compared with errors ($t_{(23)} = 3.23$; $p = 0.004$; $d = 0.69$), which was absent in the ipsilateral hemisphere ($t_{(23)} = 0.71$; $p = 0.483$; $d = 0.15$). The difference between the speeding-up of contralateral relative to ipsilateral α frequency was found to be statistically significant as well ($t_{(23)} = 2.06$; $p = 0.05$; $d = 0.44$; Fig. 4B). Results on trial matching analyses confirmed our findings, with faster α frequency for correct (11.49 Hz, SE = 0.21 Hz) relative to error trials (10.48 Hz, SE = 0.28 Hz) in the contralateral hemisphere ($t_{(23)} = 3.552$, $p = 0.001$, $d = 0.725$). Finally, as an additional control, we analyzed the accuracy effects in the entire cluster for α frequency. The results were again in line with those reported after the electrode selection procedure and trial matching. Indeed, the ANOVA showed a significant interaction of ACCURACY \times HEMISPHERE ($F_{(1,23)} = 4.467$; $p = 0.046$; $\eta_p^2 = 0.163$) with faster α frequency in the contralateral hemisphere for correct (11.14 Hz, SE = 0.34 Hz) versus erroneous responses (10.63 Hz, SE = 0.33 Hz) ($t_{(23)} = 2.82$, $p = 0.01$, $d = 0.576$). No accuracy effects emerged in the ipsilateral hemisphere ($t_{(23)} = 0.357$, $p = 0.724$, $d = 0.072$). As reported in previous studies (Samaha and Postle, 2015; Di Gregorio et al., 2022b), α frequency did not account for subjective confidence, neither using the electrode selection procedure (all p values > 0.476) nor after clustering (all p values > 0.281).

Finally, we found that between-subject differences in accuracy can be explained by the differences in contralateral speed of alpha activity, but not by changes of α amplitude across the two hemispheres (see previous paragraph). Specifically, the faster the contralateral (but not ipsilateral) alpha activity of the participant, the higher the overall task accuracy, as measured via d' score (contralateral: $r = 0.412$, CI = $[0.046, 0.715]$; ipsilateral: $r = 0.029$, CI = $[-0.459, 0.449]$, Fig. 4C). These effects were specific for d' as prestimulus α frequency could not explain interindividual differences in metacognitive performance ($r = 0.273$, CI = $[-0.260, 0.679]$), suggesting that α frequency modulations specifically impact perceptual performance but having no role in determining one's individual metacognitive ability (Fig. 4C).

Discussion

How does our subjective experience relate to objective perceptual information? How do these mechanisms interact to give rise to an integrated sense of our perceptual environment, and does this depend on whether we can predict upcoming sensory information? The present study provides information on these open questions. By use of a modified Posner paradigm and concurrent EEG recordings, we have tested what neural markers could account for objective accuracy as opposite to subjective confidence. Importantly and different to previous studies, we addressed these questions in conditions where the participant could form a prediction based on informative spatial cues. Accordingly, the main findings of our study reveal that spatial cues modulate the topographical distributions of both α frequency and amplitude, although these α parameters are dissociable as to their link to perceptual performance measures. In particular, while α amplitude reflects perceptual levels of confidence and metacognition, already before stimulus presentation, α frequency predicts perceptual accuracy and sensitivity.

The link between α amplitude and subjective confidence and metacognition has been reported in previous studies (Samaha and Postle, 2015; Benwell et al., 2017, 2022; Iemi et al., 2017). However, in these studies, stimuli are always presented at the same location, with temporal uncertainty as to when stimuli are presented. Participants entertain two alternative hypotheses consisting of one stimulus configuration (e.g., presence: 50% probability) versus another stimulus configuration (e.g., absence: 50% probability) at any given time, thus fluctuating between a more conservative or more liberal attitude toward their internal level of confidence to respond having seen one versus the other stimulus configuration. Crucially, in our study, in addition to temporal uncertainty, we have provided predictable lateralized contextual information, which was not assessed in previous research (Samaha and Postle, 2015; Benwell et al., 2017, 2022; Iemi et al., 2017; Di Gregorio et al., 2022b).

What happens when the contextual information allows for predictions of the upcoming stimulus position? Here we found that retinotopically organized α amplitude still accounts for the level of confidence reported by the participants. However, the process through which this mechanism is achieved seems to rely more tightly on the predictive level of the contextual information across the two hemifields. More specifically, the hemisphere contralateral to the cued position shows an α amplitude desynchronization accounting for a higher level of confidence, along with a synchronization of α amplitude in the ipsilateral hemisphere. An inverse relationship was found for low confidence trials. Hence, ipsilateral synchronization (together with contralateral

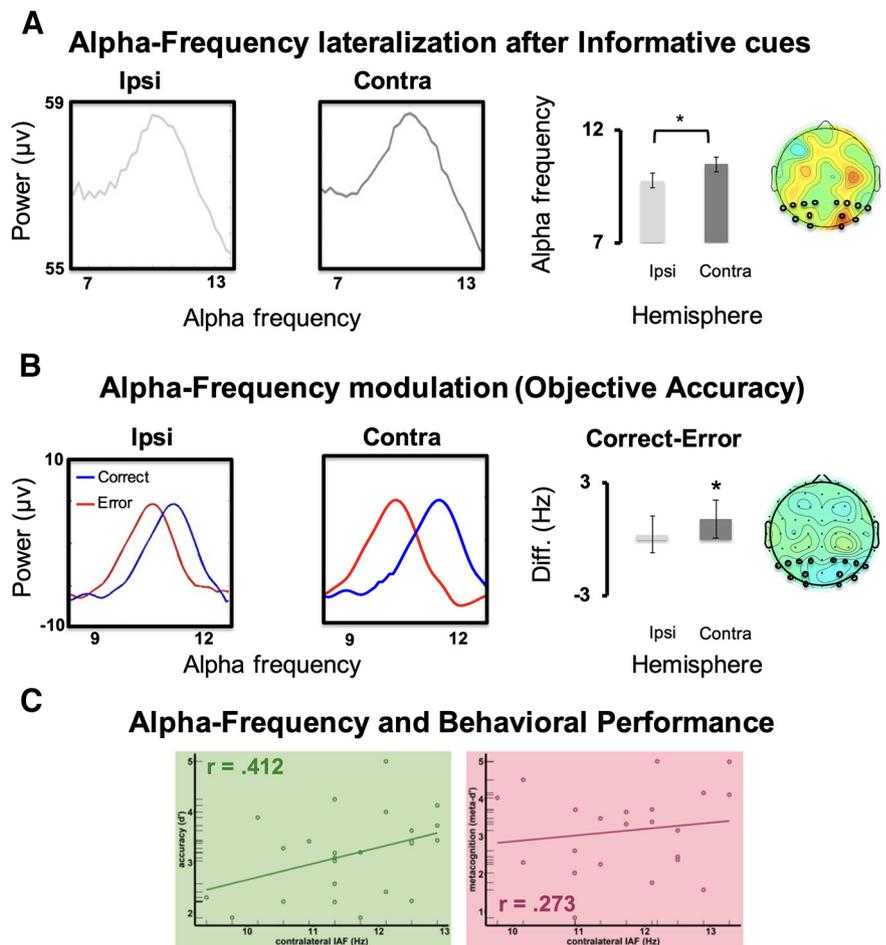


Figure 4. *A*, Prestimulus averaged α frequency (alpha band 7–13 Hz) is represented as the Z-scored mean power ($10 \cdot \log_{10}$ [mV^2/Hz]) spectrum in the cue-stimulus time period in the ipsilateral and contralateral hemispheres after informative cues. Data are reported from the peak electrodes in the ipsilateral and contralateral hemisphere. Bar graph is reported for α frequency in the ipsilateral and contralateral hemispheres. Topography represents the α frequency distribution over electrodes (electrodes are flipped to have contralateral activity in the right-hand side and ipsilateral activity in the left-hand side). Black circles represent selected electrodes. *B*, Prestimulus averaged α frequency in the cue-stimulus time period for the contralateral and the ipsilateral electrodes and for correct and error trials within the alpha band. Data are reported from the peak electrodes in the ipsilateral and contralateral hemisphere. Bar graph is reported for normalized power in the ipsilateral and contralateral hemispheres for the difference Correct – Error. Topography represents the difference between Correct and Error trials (electrodes are flipped to represent contralateral activity in the right-hand side and ipsilateral activity in the left-hand side). Black circles represent selected electrodes. *C*, Correlation between α frequency and behavioral performance for accuracy (d' measure) and metacognition (meta- d' measure). $*p < 0.05$ (two-tailed t test). Error bars indicate SEM. Diff, Difference. Hz, Herz; μV , microvolts.

desynchronization) in high confidence trials reflects the informed hypothesis not to attend (or actively inhibit) irrelevant information that may be presented ipsilaterally, favoring contralateral sensory processing (Thut et al., 2006; Klimesch et al., 2007). Contralateral synchronization (together with ipsilateral desynchronization) to low confidence trials reflects a failure to allocate resources according to the predictive hypothesis. In other words, the perceptual hypotheses about stimulus location seem to be reflected in the retinotopically distributed α amplitude in the visual cortex that would follow these expectations (i.e., desynchronized alpha activity in the contralateral hemisphere). Therefore, the level of desynchronization of these α cycles seems to mark the strength of the prior hypothesis (the strength of the feedback mechanism). In case of an informative cue, strong *a priori* hypotheses are beneficial as they successfully predict stimulus occurrence in most of the cases, eventually leading to high overlap between expectance and occurrence, reflected in high accuracy in estimating our perceptual states (i.e., metacognitive accuracy).

Analyses performed on metacognitive abilities confirmed these results at the between-subject level, where contralateral changes of prestimulus α amplitude selectively accounted for metacognitive abilities of participants, but not their perceptual sensitivity. Here, metacognition can be defined as the ability to assess the accuracy of our internal perceptual states, thus representing postperceptual decision-making process, rather than subjective perceptual bias.

In Di Gregorio et al. (2022b), under uninformative cue conditions, prestimulus α amplitude accounted for confidence levels but not metacognitive performance; and only poststimulus α amplitude accounted for metacognitive performance. We interpreted this as the result of sensory input updating the internal representation of the stimulus, once the stimulus was presented. Here, under informative cue conditions, we found that contralateral prestimulus α amplitude accounted for metacognitive abilities already before the stimulus was presented. Thus, the informative cue was used to anticipate stimulus appearance at the cued location so as to maximize performance and minimize the error, in line with a predictive coding account (Friston and Kiebel, 2009).

In accordance with our previous results, we found that α frequency consistently accounts for objective accuracy with faster α frequency accounting for better performance. Importantly, depending on the predictability of forthcoming stimulus location, α frequency can be modulated evenly as shown previously (Di Gregorio et al., 2022b) or over the hemisphere coding for the predicted location as demonstrated here, by enhancing sampling resources at the attended location and thus maximizing in the latter case the possibility to correctly report the presence of a target at expected position. Importantly, these effects can be observed at a between-subject level, where perceptual sensitivity, as measured via d' , is directly and selectively related to contralateral speed of alpha activity, such that the faster the α frequency over the hemisphere covering the attended location, the higher perceptual sensitivity at that position. Therefore, given visual resource limitations (Fries et al., 2001), we infer that the more one can predict the exact location of the forthcoming stimulus, the higher will be the resource allocation at that particular point in space translating in higher α (sampling) frequencies in the corresponding visual areas. Indeed, recent evidence is in line with this interpretation, demonstrating flexible retinotopically organized changes of α frequency during temporal processing and spatial attention deployment. Specifically, a recent study (Sharp et al., 2022) showed that stimuli integration versus segregation was related to slower versus faster α frequency contralateral to an attended location, thus confirming the role of α frequency as a general sampling mechanism that can be strategically tuned by deployment of spatial attention.

It has been proposed that the relationship between α amplitude and accuracy reflects a top-down control process (Worden et al., 2000; Capotosto et al., 2009; Marshall et al., 2015; van Diepen et al., 2016) that allocates limited attentional resources toward the relevant location, thus actively ignoring irrelevant spatial locations (Jensen and Mazaheri, 2010; Slagter et al., 2016). Moreover, the role of this controlled deployment of attentive resources has been suggested to reflect a biasing signaling toward the forthcoming stimulus (Landau and Fries, 2012; Landau, 2018; Re et al., 2019). However, whether α amplitude reflects an expression of perceptual bias or can also directly account for objective accuracy remained a matter of debate (Linkenkaer-Hansen et al., 2004; Rajagovindan and Ding, 2011; Snyder et al., 2016). Our data are in line with recent evidence proposing that prestimulus α

amplitude encodes biases of upcoming sensory decisions induced by top-down predictions (Mayer et al., 2016; Tarasi et al., 2022). How can we then explain the fact that α amplitude also accounts for objective accuracy? Our data show that α amplitude does encode biases of upcoming sensory predictions based on top-down prediction, but crucially, the predictability of the contextual information will render the bias as predictive as the effective sensory occurrence itself, resulting in a substantially overlapping measure. Yet, the critical point we clarify here, for the first time, is that it rather reflects the level of top-down induced bias and not the level of accuracy per se. Put otherwise: highly predictable target locations will enforce top-down predicting indices (α amplitude) accounting for a high level of confidence, thus highly overlapping with the level of accuracy. This bias organizes sensory resources toward the most plausible prediction by modulating in turn oscillatory α frequency. To sum up: lateralization of prestimulus α amplitude accounts for metacognitive abilities already before stimulus presentation, but not for the enhanced stimulus sensitivity. The latter can be best explained by the allocation of sensory sampling exclusively at the to be attended location, namely, a speeding up of alpha oscillation allowing for higher sampling rate.

In conclusion, we show here that modulation of attention in space allocates faster sampling capacity (faster α frequency) and sensory bias (α amplitude) exclusively at the attended location to match what we think we see with what is most likely to be out there, thus maximizing the efficiency of our conscious experience.

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