Behavioral/Cognitive

Spontaneous Alpha-Band Oscillations Bias Subjective Contrast Perception

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Perceptual decisions depend both on the features of the incoming stimulus and on the ongoing brain activity at the moment the stimulus is received. Specifically, trial-to-trial fluctuations in cortical excitability have been linked to fluctuations in the amplitude of prestimulus \( \alpha \) oscillations (\( \sim \)8–13 Hz), which are in turn associated with fluctuations in subjects’ tendency to report the detection of a stimulus. It is currently unknown whether \( \alpha \) oscillations bias postperceptual decision-making, or even bias subjective perception itself. To answer this question, we used a contrast discrimination task in which both male and female human subjects reported which of two gratings (one in each hemifield) was perceived as having a stronger contrast. Our EEG analysis showed that subjective contrast was reduced for the stimulus in the hemifield represented in the hemisphere with relatively stronger prestimulus \( \alpha \) amplitude, reflecting reduced cortical excitability. Furthermore, the strength of this spontaneous hemispheric lateralization was strongly correlated with the magnitude of individual subjects’ biases, suggesting that the spontaneous patterns of \( \alpha \) lateralization play a role in explaining the intersubject variability in contrast perception. These results indicate that spontaneous fluctuations in cortical excitability, indicated by patterns of prestimulus \( \alpha \) amplitude, affect perceptual decisions by altering the phenomenological perception of the visual world.

Key words: alpha oscillations; appearance; attention; lateralization; perceptual bias; subjective perception

Significance Statement

Our moment-to-moment perception of the world is shaped by the features of the environment surrounding us, as much as by the constantly evolving states that characterize our brain activity. Previous research showed how the ongoing electrical activity of the brain can influence whether a stimulus has accessed conscious perception. However, evidence is currently missing on whether these electrical brain states can be associated to the subjective experience of a sensory input. Here we show that local changes in patterns of electrical brain activity preceding visual stimulation can bias our phenomenological perception. Importantly, we show that the strength of these variations can help explain the great interindividual variability in how we perceive the visual environment surrounding us.

Introduction

Perception is not only determined by external stimuli but is also shaped by ongoing internal brain states at the moment of stimulus presentation. A specific type of ongoing brain signals are so-called \( \alpha \) oscillations with a frequency of \( \sim \)10 Hz, which are most dominant in visual cortical areas. Alpha oscillations reflect a state of reduced cortical excitability, indicated by an inverse relationship with single-unit firing rates (Haegens et al., 2011; Chapeton et al., 2019), multi-unit activity (Bollimunta et al., 2008; Van Kerkoerle et al., 2014), or the fMRI BOLD signal (Goldman et al., 2002; Mayhew et al., 2013). In line with this inhibitory function, the power of \( \alpha \) oscillations in the moment just before stimulus presentation affects the detection of near-threshold visual stimuli (Ergenoglu et al., 2004; Van Dijk et al., 2008; Lange et al., 2013). Specifically, strong alpha power induces a conservative detection bias, rendering observers less likely to report having seen a stimulus (Limbach and Corballis, 2016; Iemi et al., 2017; Samaha et al., 2020a). These studies raise a fundamental question about the effect of prestimulus \( \alpha \) oscillations on perceptual decision-making: do fluctuations of cortical excitability reflect changes only in strategic decisions to report stimulus presence, or do they affect how the visual stimuli are subjectively perceived?

A similar question has been raised regarding spatial attention, which is known to improve behavior accuracy; is this improvement associated with a change in the subjective appearance of attended stimuli? To address this question, Carrasco et al. (2004)
developed a paradigm in which observers are presented with two Gabor patches: a standard patch with a fixed contrast and a test patch whose contrast varies across trials. Observers report the patch with higher apparent contrast, resulting in a psychometric function (PMF) indicating the probability of reporting the test patch as a function of the test’s relative contrast. Numerous studies have demonstrated that the contrast at which the test stimulus appears similar to the standard is shifted by attentional cues such that attended stimuli appear subjectively more contrasted (Carrasco and Barbot, 2019). Here, we adapted this paradigm to test whether cortical excitability indicated by prestimulus α oscillations has a similar effect.

We leveraged the fact that alpha power is often lateralized across the left and right cortical hemispheres. When spatial attention is cued to a lateral location, alpha power decreases in the contralateral relative to the ipsilateral hemisphere (Worden et al., 2000; Thut et al., 2006), indicating greater excitability in the task-relevant hemisphere and greater inhibition in the task-irrelevant hemisphere (Jensen and Mazaheri, 2010). Importantly, such lateralization can also occur spontaneously in the absence of external cues, driven only by internal fluctuations in the deployment of spatial attention (Bengson et al., 2014; Boncompte et al., 2016). Thus, our aim was to test whether subjective contrast appearance is amplified by such spontaneous prestimulus lateralization. To this end, we used the comparative contrast judgment task developed by Carrasco et al. (2004), but without attentional cues. Thus, instead of comparing contrast judgments relative to a cued location, contrast judgments were compared relative to the hemisphere with stronger alpha power. Thereby, we asked observers about their subjective contrast perception directly, rather than inferring their subjective perception from detection hit rates. Moreover, since the task did not require detection of near-threshold targets, a strategic decision bias to report stimulus presence could be excluded.

We found that stimuli preceded by reduced contralateral compared with ipsilateral α amplitude appeared as stronger contrasted. For comparison, we included an additional task with symbolic attentional cues inducing typical lateralization and found a striking similarity between cue-induced and spontaneous lateralization. A time-resolved logistic regression analysis further showed that trial-by-trial fluctuations in lateralized α amplitude in the moment before stimulus onset biased contrast perception, whereas nonlateralized α amplitude had an independent effect on objective accuracy. Finally, we found that the strength of spontaneous lateralization patterns significantly correlated with individual participants’ idiosyncratic biases.

Materials and Methods

Participants

Forty-six participants took part in the experiment. Two of them were excluded because of performance <2 SDs from the population mean in the contrast discrimination task, and four were excluded for noisy EEG signal. This left us with 40 participants (female = 26, mean age = 23 years, age range = 18-34 years, 34 right handed). The final sample size had been determined in advance, based on the previous works investigating similar research questions (Iemi et al., 2017; Iemi and Busch, 2018). The sample size in these studies was marginally lower than in the current study (between 25 and 33 subjects), but with a high number of trials per participant (between 700 and 1400). In the current experiment, we opted to have less trials (576 in the main experimental condition), but more participants. This trade-off between trial number and sample size in ensuring adequate statistical power has been detailed by Baker et al. (2021). All participants were compensated for participation with course credit or money (8 EUR/h). The study was approved by the ethics committee of the faculty of Psychology and Sports Science, University of Münster. All participants gave their written consent to participate.

Apparatus

Recordings took place in a dimly-lit, soundproof cabin. Participants placed their heads on a chin-rest and could adjust the height of the table to be seated comfortably. Stimuli were generated using MATLAB 2019a (www.mathworks.com) and the Psychophysics Toolbox 3 (Brainard, 1997; Kleiner et al., 2007). The experiment was controlled via a computer running Xubuntu 16.04, equipped with an Intel Core i5-3330 CPU, a 2 GB Nvidia GeForce GTX 760 GPU, and 8 GB RAM. The experiment was displayed on a 24 inch Viewpixx/EEG LCD Monitor with 120 Hz refresh rate, 1 ms pixel response time, 95% luminance uniformity, and 1920 × 1080 pixels resolution (www.vpixx.com). Distance between participant eyes and the monitor was ~86 cm.

Stimuli and experimental procedure

All stimuli were presented on a gray background (52.24 cd/m²). Each trial started with a fixation point, a small circle (diameter 0.1 dva) surrounded by four diagonal sectors of a bigger circle (diameter 0.6 dva) of a dark gray (6.5 cd/m²). Simultaneously with the fixation point, two placeholders of the same color were displayed, with an edge of 6.5 dva indicating the area of subsequent appearance of the Gabor, and were centered at ±8.88 dva on the horizontal and at −4.6 dva on the vertical meridian, where all coordinates are referred to the center of the screen. Hence, the placeholders and the stimuli appeared at 10 dva of eccentricity, in the lower visual field. The fixation and the placeholders remained on the screen for the whole duration of the trial. After a variable SOA (uniformly sampled between 2100 and 3300 ms), two Gabor patches (diameter = 6 dva; spatial frequency = 2 cpd) appeared for 41.67 ms (5 frames) in the positions delimited by the placeholders.

In the contrast discrimination task, the Gabor patches both had vertical orientations. One stimulus (standard) had a Michelson contrast of 0.2, whereas the other (test) could be in the range [−0.45, 0.45] log10 units around the standard stimulus contrast. The contrast of the test stimulus was determined on a trial-by-trial basis by a Bayesian adaptive procedure implemented ad hoc for the present experiment (see next paragraph). After the stimuli disappearance the participants had to report in which hemifield (left or right) the stimulus with the highest contrast had appeared.

In the orientation discrimination task, 1200 ms before stimulus appearance one of the lower sections (left or right) of the fixation point was increased in luminance (78.39 cd/m²) for 200 ms, indicating the position to be attended for reporting the orientation of the stimulus target. The stimuli consisted of 2 Gabor patches which had the same Michelson contrast (0.2) of the standard stimulus as defined before, but an orientation of ±45° with respect to the vertical axis. After the stimuli disappearance, the participants had to report the orientation (left, counterclockwise; right, clockwise) of the cued stimulus. For both tasks, participants were invited to provide their responses with their dominant hand by pressing left or right arrow keystroke on a standard German layout keyboard.

Throughout the whole experiment, each participant completed 768 trials, consisting of 192 trials for orientation discrimination and 576 trials for contrast discrimination task. Of the latter, half were showing the test stimulus on the left hemifield and the other half on the right hemifield. The proportion of trials for each task (and for each hemifield probed) was maintained constant in the 8 blocks of 96 trials each. The order of the trial sequence was randomized. Every 24 trials, a summary feedback on performance was provided to the participant: such feedback was given collapsing together the orientation and contrast discrimination task, but was not taken into account those trials in which the choice was arbitrary (i.e., the standard and the test stimulus had the same contrast), since no definition of “correct response” could apply.

Bayesian adaptive procedure

In order to adapt the contrast of the stimuli online during the experiment, we implemented a custom Bayesian adaptive procedure...
in MATLAB following the guidelines detailed by Baek et al. (2016) and Watson (2017). First, we defined a model that could proficiently describe the probability of response toward the test stimulus. We individuated this model in a modified version of the logistic PMF as follows:

\[ P_{\text{resp}} = \lambda + \frac{1 - 2\lambda}{1 + 10^{-\beta(x - \text{PSE})}} \]  (1)

Where \( x \) is the contrast of the test stimulus compared with the standard, \( \lambda \) is the asymptotic value, \( \beta \) describes the slope of the PMF, and \( \text{PSE} \) is the point of subjective equality. It is possible to notice that, in the current formulation, \( \lambda \) describes both the low and the upper asymptotic value: this choice was made to stabilize the contrast probing on both the upper and the lower sides of the sigmoid in equal measure. Furthermore, during the online estimation, the \( \lambda \) value was set constant, to limit the amount of trials used to probe the extrema of the PMF.

In order to implement the adaptive procedure, we defined a two-dimensional \( \theta = (\text{PSE}, \beta) \) parameter space that represents all potential observable PMFs for each combination of parameters and a one-dimensional stimulus search space over a range of possible contrasts for the test stimulus. Regarding the parameter space, values for \( \text{PSE} \) were selected in a range between -0.3313 and 0.3313, leading to 41 equally spaced values on a logarithmical scale. Fifty-one equally spaced values for \( \beta \) were selected in a range between 1.22 and 10.88, whereas \( \lambda \), as anticipated, was set constant at a value of 0.02. The ranges for the \( \text{PSE} \) and \( \beta \) parameters were chosen to encompass 0.99 CIs of the parameter distributions obtained by fitting the model on pilot data. The contrast values were defined as 31 equally spaced log units in a range between -0.45 and 0.45 around the standard contrast (log10(0.2)). The procedure was implemented separately for the two visual fields.

**Online fixation control**

Eye movements were monitored using a desktop-mounted Eyelink 1000+ infrared-based eye-tracking system (www.sr-research.com) set to 500 Hz sampling rate (binocular). The eye tracker was (re)calibrated using a 9 point calibration grid at default locations. Participants were required to keep their gaze on the fixation symbol throughout the trial, until the end of stimulus presentation. To ensure steady fixation and to avoid ocular or preferential encoding of one of the targets, a trial was aborted and repeated at the end of the respective block whenever participants blinked or gaze was outside of a 2.5° radius around the fixation symbol. The eye tracker was recalibrated at the start of each block and whenever participants lost fixation for more than three consecutive times, causing the restart of the trial.

**EEG recording and preprocessing**

EEG was recorded with a Biosemi Active Two EEG system with 65 Ag/AgCl electrodes (www.biosemi.nl), set to 1024 Hz sampling rate. Sixty-four electrodes were arranged in a custom-made montage with equidistant placement (EasyCap M34; www.easycap.de), which extended to more inferior areas over the occipital lobe than the conventional 10-20 system (Oostenveld and Plesmanstra, 2001). An additional external electrode was placed below the left eye. EEG data were preprocessing performed using MATLAB R2018a (www.mathworks.com) and the EEGLab toolbox (Delorme and Makeig, 2004), with the Cleanline (Mullen, 2012) extension. Data were resampled to 512 Hz, high-pass filtered at 1 Hz, low-pass filtered at 70 Hz, and notch-filtered between 48 and 52 Hz. Subsequently, data were rereferenced to a robust reference (Bigdely-Shamlo et al., 2015). Vertical and horizontal electrooculograms were derived from two electrodes above and below the left eye, and two electrodes at the lateral canthi of both eyes, respectively. Continuous data were segmented into epochs from 2000 ms before target onset to 500 ms after stimulus onset. To automatically clean the EEG signal from noisy segments, we applied a two step procedure. As a first step, to select artifacts coming from single electrodes in single trials we z-scored the EEG data for each trial along the channel dimension, and interpolated single segments exceeding an absolute z value of 6. When a channel was interpolated for more than the 15% of the trials, then it was interpolated for all the trials. As a second step, epochs with irregular artifacts were automatically detected and rejected using a combination of threshold criterion, joint probability, or high power in higher-frequency bands (40-70 Hz) indicating muscular noise. When the amount of data either interpolated or rejected exceeded the threshold of 15%, the data from a subject were discarded, as we preregistered. On average, the 7.45±2.409% (mean± SD) of the data were either interpolated or discarded. Remaining artifacts were corrected using independent component analysis. After independent component analysis, all electrodes were rereferenced to common average.

**EEG data analysis**

*Prestimulus difference in time-frequency analysis.* As a first step, we aimed to characterize the prestimulus pattern associated with cue-induced lateralization. This was first achieved with a wavelet transform in fieldtrip (Oostenveld et al., 2011). The wavelet analysis was performed for frequencies ranging from 3 to 40 Hz, each wavelet increasing linearly from 3 to 8 cycles, and sampling every 1 Hz and every 15.6 ms. We selected a set of five occipital channels per hemifield that maximized the expected effect of cue-induced lateralization in the alpha band. This subset of left and right channels was then used to compute the spontaneous lateralization in the contrast discrimination task.

*Prestimulus difference in instantaneous amplitude.* We conducted a spectral analysis to evaluate the patterns of \( \alpha \) lateralization immediately preceding the stimulus presentation, for both the contrast discrimination task and the attention localizer. In order to exclude any potential leak of poststimulus activity in the prestimulus window, and to limit edge artifacts because of filtering and to the Hilbert transform, for each trial, we applied the following steps:

1. Selection of time window of interest [-500; 0] ms from stimulus onset.
2. Expansion of the signal by mirroring both tails for the first/last 195 ms.
4. Application of Hilbert transform, and extraction of instantaneous amplitude by taking the absolute value of the complex signal.
5. Selection of the original portion of the signal.

We baseline the signal by subtracting, for each time point and each trial, the average amplitude of all channels. Next, for each experimental condition (orientation or contrast discrimination), we averaged together the trials belonging to “left” or “right” categories (cue direction or response, respectively, for the task), and computed the difference for all channels. In order to compute lateralization, we selected a subset of 5 channels per hemifield, and we compared the averaged time courses of left and right channels. We computed the difference between the averages of left and right channels. We were in this way able to obtain, for each single participant and each experimental condition, the time course of \( \alpha \) lateralization, between comparisons of interest. Most importantly, a positive sign of this time course indicated an increase in \( \alpha \) ipsilateral to participants’ response, or cued location. Statistical significance was evaluated with one-sample \( t \) test against 0. To correct for multiple comparisons, we performed a cluster permutation test, where clusters were defined by contiguity in the time domain: for 10,000 repetitions, we multiplied a random participants subset by -1, we computed the cluster statistic by selecting all the contiguous points with \( p < 0.05 \), creating distribution of randomly generated cluster statistics (Samaha et al., 2017). Then we computed the empirical cumulative distribution function for the random distribution, and we individuated the probability value for the cluster statistic obtained with the nonshuffled data. We rejected \( H_0 \) when the cluster statistics was exceeding the 95 percentile of permutations, which is equivalent to a one-tailed test. This choice was motivated by the specific directionality expected in the typical cue-induced lateralization (Worden et al., 2000; Thut et al., 2006; Rihs et al., 2007), which features an increase in \( \alpha \) amplitude ipsilateral and a decrease contralateral to the cue direction. The same rationale was adopted for the contrast discrimination task, where a specific directionality of this effect was motivated by an *a priori*
hypothesis according to which higher alpha power in one hemisphere, being associated with decreased excitability, would decrease responsiveness to visual stimulation and hence be associated with reduced perceived contrast for the stimulus represented in the contralateral hemifield.

Similarity between cue-induced and spontaneous lateralization. We aimed to test whether the spontaneous lateralization associated with a subjective contrast report was similar to the cue-induced lateralization in conditions of high perceptual uncertainty. To this end, we first computed topographical similarity between cue-induced and spontaneous lateralization via matrix multiplication. So, for each participant, let W be the $N_{channels} \times M_{topo}$ produced by the difference between left and right cue, and X the matrix (of same size), produced by the difference in the response, similarity was computed as follows:

$$S = W'X$$

Where’ indicates matrix transpose. This leads to a $M_{topo} \times M_{topo}$ matrix, which shows how similar the two patterns across the whole time window are.

Notably, we evaluated the difference in similarity between trials where the perceptual uncertainty was higher versus those trials in which the perceptual uncertainty was lower. We defined perceptual uncertainty based on the inverse of the PMF in Equation 1 as follows:

$$Contrast = \frac{1}{\beta} \log_{10} \left( \frac{1 - P_{topo} - \lambda}{P_{topo} - \lambda} \right) + PSE$$

In this way, we were able to select the trials whose contrast difference between test and standard stimulus was belonging to the range of contrasts around the threshold ($p = 0.5 \pm 0.25$, “high uncertainty”) and the ones outside this range, defined as “low uncertainty.” For each of the two groups of trials, within each participant, we computed the difference between left and right cue, and the difference in response as described before. Based on Equation 2, we evaluated whether the “high uncertainty” trials ($X_{high}$) were showing a stronger similarity to the cue induced lateralization than the “low uncertainty” ($X_{low}$):

$$S_{diff} = W'X_{high} - W'X_{low}$$

At the group level, we tested whether this difference was different from 0 with one-sampled t tests on the whole similarity matrix. We corrected for multiple comparisons via a cluster permutation approach analogous to the one defined before but applied this time on the similarity matrix instead of a time series. We rejected $H_0$ when the cluster statistic was exceeding the 95th percentile of permutations, which is equivalent to a one-tailed test. The choice of a one-tailed test is theoretically motivated. Previous evidence shows that attentional modulation of perceived contrast is stronger around the PSE (Carrasco et al., 2004; Carrasco and Barbot, 2019; Ithipuripat et al., 2019). For this reason, we expected patterns of spontaneous α lateralization associated with subjective contrast report to be stronger, and more similar to the one induced by the cue, when the perceptual uncertainty was at its peak.

Logistic regression analysis. In order to analyze the effect of trial-by-trial variations in prestimulus alpha band amplitude on perceptual contrasts while controlling for objective contrast differences, we used a logistic regression analysis. Preprocessing steps preliminary to the logistic regression analysis include three additional steps, so we expand here the procedure already described above:

1. Selection of time window of interest [-500; 0] ms from stimulus onset.
2. Expansion of the signal by mirroring both tails for the first/last 195 ms.
4. Downsampling to 128 Hz, to decrease computation time.
5. Application of Hilbert transform, and extraction of instantaneous amplitude by taking the absolute value of the complex signal.

6. Selection of the original portion of the signal.
7. Rank scoring across trials to mitigate the effect of outliers.
8. z scoring across trials in order to obtain normalized β scores from the model.

Importantly, the last step (z scoring) was applied to all models’ regressors. The model was defined as a typical logistic regression model in the following form:

$$P_{topo} = \frac{1}{1 + \exp(-X_{model})}$$

$$X_{model} = \beta_0 + \beta_1 \Delta contrast + \beta_2 \text{amplitude} + \beta_3 \Delta contrast \ast \text{amplitude}$$

Our model consisted of four different regressors as described in Equation 5b: $\beta_0$, indicating the overall tendency to respond toward one or the other hemifield independently from the actual contrast of the stimuli and underlying brain activity; $\beta_1$, the weight that the physical contrast difference between stimuli had in determining the outcome of the decision process; $\beta_2$, the weight of prestimulus $\alpha$ amplitude; and $\beta_3$, the weight for the interaction between physical contrast difference and prestimulus $\alpha$ amplitude. Logistic regression coefficients were computed via iterative reweighted least square (Bishop and Nasrabadi, 2006), for each combination of electrode and time point for the whole prestimulus window. The application of the model yielded hence for each participant a $N_{channels} \times M_{topo} \times 4$ regressors for each subject.

At the group level, we tested whether the weights for the prestimulus $\alpha$ amplitude and the interaction between $\alpha$ amplitude and physical contrast difference were significantly different from 0. For this purpose, we first ran a one-sample $t$ test against 0, for each channel, time point, and regressor. We defined clusters by selecting those t values exceeding the critical threshold ($\alpha = 0.05$) on both tails. From each cluster, we obtained a cluster statistic by summing together all the t values belonging to the cluster, that is, characterized by contiguity in space (electrodes) and time. To correct for multiple comparisons, for 1000 repetitions, we multiplied a random participants subset by $-1$, and repeated the above-mentioned steps to obtain a distribution of cluster statistics under the null hypothesis. We rejected the null hypothesis if a cluster statistic was $<2.5\text{th}$ or $>97.5\text{th}$ percentiles of the permutations. In order to maintain a consistent Type I error threshold of $\alpha = 0.05$ for both one-tailed and two-tailed tests across the whole manuscript, we first transformed the p values exceeding the median as $1 - p$. Both values were then multiplied by 2, so that the magnitude of the p value of this two-tailed test could be evaluated against a significance threshold of 0.05 and not any longer to 0.025.

Correlation between spontaneous lateralization and individual PSEs. We further aimed to investigate whether the spontaneous patterns of $\alpha$ lateralization associated with subjective contrast report were correlated with the observers’ idiosyncratic biases. This was done by first computing PSEs according to Equation 3, by defining $p = 0.5$, for each participant and visual field. We aggregated the PSEs between visual fields as follows:

$$PSE_{left} = -0.5(PSE_{left} - PSE_{right})$$

where $PSE_{left}$ and $PSE_{right}$ are the perceptual thresholds estimated for the left and right visual field, respectively, and $PSE_{diff}$ is the aggregated one. The sign correction was applied to maintain consistency across the results, so that negative values indicate bias toward the right hemifield, and vice versa.

As a second step, we followed the same procedure used to evaluate the spontaneous patterns of lateralization already described before (see Prestimulus difference in instantaneous amplitude), consisting of the difference between left and right occipital channels in the contrast between left and right response. This yielded a time course of strength and directionality of $\alpha$ lateralization, that we correlated with the PSE of the
participants, for each time point in the prestimulus window. This yielded a time series of correlations spanning the 500 ms before stimulus onset. We tested for multiple comparison by first identifying the cluster showing contiguous timepoints with $p < 0.05$ (two-tailed), and summing up the $r$ values for all the points in the cluster to obtain a relative cluster statistic. Then, for 1000 times, we shuffled the vector of PSEs and repeated the steps before to obtain a distribution of cluster statistics under the null hypothesis. We rejected the null hypothesis if a cluster statistic was $>2.5$th or $<97.5$th percentiles of the permutations. In order to maintain a consistent Type I error threshold of $\alpha = 0.05$ for both one-tailed and two-tailed tests across the whole manuscript, we multiplied the cluster $p$ values by 2, so that the magnitude of the $p$ value of this two-tailed test could be evaluated against a significance threshold of 0.05 and not any longer to 0.025.

**Quantification of effect sizes in cluster permutation tests**

In order to provide a metric of effect size for cluster permutation tests, we adopted the procedure suggested by Meyer et al. (2021) as follows. For each cluster, we computed the effect size measure of interest (Cohen’s $d$ for $t$ test, Pearson’s $r$ for correlation) (Cohen, 1988) for each time point/channel entry in the cluster, and averaged this metric across the whole cluster. These measures are reported together with the cluster $p$ values, as cluster $d$ and cluster $r$, respectively.

**Results**

Human observers ($N = 40$) performed a contrast discrimination task (Fig. 1). Two Gabor patches were presented on each trial: one in the lower left and another in the lower right visual field. One of the patches had a fixed contrast (standard), while the contrast of the other patch (test) was selected from a range around the standard’s contrast. Observers reported which of the patches appeared to have the highest contrast, resulting in a PMF describing the probability of reporting the test patch as a function of the test’s relative contrast. Test contrasts were determined trial by trial by an adaptive Bayesian algorithm, which selected the test contrast that would be most efficient for estimating the PMF based on the data collected so far (see Materials and Methods). In a separate cued orientation discrimination, from hereafter named “attention localizer,” the Gabors were preceded by a symbolic cue indicating the location of the to-be-attended and to-be-reported target. Observers reported the orientation of the target patch (45° or –45°).

![Figure 1](https://example.com/figure1.png)

**Behavioral results**

Participants performed well in both tasks, achieving a performance of $0.748 \pm 0.091$ (mean $\pm$ SD) in the contrast discrimination task (averaged across all test contrasts) and $0.978 \pm 0.03$ in the attention localizer task. A comparison of accuracy in the contrast discrimination task between first and second half of the experiment showed a small, but consistent, increase in accuracy in the second half of the experiment ($t_{(39)} = -4.383, p < 0.001$, two-tailed, $d = -0.693$). This effect might have been induced by progressive training in the task.

For the contrast discrimination task, we used data from all trials to re-estimate parameters of a PMF, namely the PSE and
slope, describing for each observer the probability of choosing the left patch as the most contrasted as a function of the contrast difference between the left and right patch (Fig 1B). While individual observers showed a general preference for choosing patches either in the left or right hemifield, these preferences were balanced across observers. Thus, the resulting average PMF was almost perfectly centered on a contrast difference of zero, indicating no systematic bias toward either hemifield.

The distribution of absolute contrast differences was balanced across hemifields, such that trials with stronger contrast in the left hemifield were stronger by the same magnitude as trials with stronger contrast in the right hemifield (Fig 1C). This symmetry was confirmed by a two-tailed t test comparing absolute contrast differences between trials with stronger contrast in the left versus right hemifield ($t(20,903) = -0.114$, $p = 0.909$, two-tailed). As a result of the adaptive Bayesian procedure, the majority of trials featured small, but nonzero contrast differences, and these differences were of the same magnitude in the left and right hemifield (Fig 1C). Second, we only analyzed the prestimulus time range, uncontaminated by the neural poststimulus response (see Materials and Methods). Thus, any prestimulus differences between poststimulus left-reports and right-reports are necessarily independent of objective stimulus contrast.

At each frequency, we computed lateralization as the amplitude difference between a group of left minus right occipital channels, and compared this lateralization between trials in which the left versus right patch was reported as more contrasted. This comparison showed a positive difference in lateralization between left and right reports, starting $\sim 200$ ms before stimulus onset (Fig 2C), indicating that, in both conditions, $\alpha$ amplitude was reduced at channels contralateral compared with ipsilateral to the patch reported as more contrasted.

To confirm this result statistically, we bandpass filtered the data in the alpha band, obtained instantaneous amplitude with a Hilbert transform, and computed again the difference between left and right occipital channels in the contrast between left and right responses, as described above. Similar to the time-frequency analysis, this contrast, whose sign indicates the direction of lateralization, was positive in the interval just before stimulus onset. A nonparametric cluster permutation test yielded a cluster of significant nonzero lateralization (cluster $p = 0.025$, one-tailed, cluster $d = 0.348$) starting at $-214$ ms before stimulus onset (Fig 2C, red horizontal bar). This result confirms that $\alpha$ amplitude was significantly reduced in the cortical hemisphere contralateral to the patch reported as more contrasted. This analysis was conducted on data from which any poststimulus data points were removed (see Materials and Methods). Thus, while this prestimulus effect occurred just before stimulus onset, it cannot be explained by temporal smearing of poststimulus signals into the prestimulus time range. Cue-induced
lateralization in the attention localizer task showed a similar, but stronger and more sustained effect (cluster \( p \leq 0.001 \), one-tailed, cluster \( d = 0.718 \)).

Previous works (Slagter et al., 2016; Newman et al., 2017; Benwell et al., 2018; Keitel et al., 2018) reported systematically higher alpha power over the right hemisphere in healthy young participants. We explored the presence of this effect in our sample, but we did not find significant evidence for systematic rightward lateralization (\( t_{(39)} = -1.22, p = 0.11 \), one-tailed). This result goes hand in hand with a lack of a systematic hemifield bias in contrast perception at the population level (Fig. 1B).

If, as hypothesized, spontaneous patterns of \( \alpha \) lateralization are related to a change in subjective perception analogous to changes produced by spatial attention shifts, it is reasonable to expect higher similarity between spontaneous and cue-induced \( \alpha \) lateralization under maximal perceptual uncertainty (i.e., for contrast values around the PMF’s midpoint). To test this prediction, for each participant, we split the trials in high and low uncertainty in the contrast discrimination task based on the individual PMF (Fig. 3B; see Materials and Methods) and computed for each set of trials lateralization as the difference between left and right choices, as described before. We then computed the similarity matrix between the pattern elicited by the attention localizer task and the prestimulus pattern associated to the response both in high and low uncertainty.

This comparison of the similarity matrices in these two different perceptual uncertainty conditions yielded a significant cluster (cluster \( p = 0.037 \), one-tailed, cluster \( d = 0.371 \)), centered at \(-200\) ms prestimulus for the contrast discrimination task but spanning almost the whole time window for the attention localizer task (Fig. 3B). This result implies that, under high perceptual uncertainty, the appearance of one stimulus as more contrasted is preceded by a short-lived lateralization of \( \alpha \) amplitude, whose topographical pattern is similar to the conventional cue-induced lateralization pattern.

**The influence of prestimulus \( \alpha \) amplitude on trial-by-trial perceptual decision-making**

While the previous analyses compared prestimulus lateralization between conditions defined by the subject’s poststimulus choices in the contrast discrimination task, the hypothesized chain of causality is actually the opposite: prestimulus brain states may bias poststimulus choices. However, the analysis of effects of prestimulus lateralization on decisions must account for the additional effect of objective contrast differences. Therefore, to analyze the effect of trial-by-trial variations in prestimulus \( \alpha \) band amplitude on perceptual decisions while controlling for objective contrast differences, we used a logistic regression analysis, which modeled the probability of reporting the left stimulus as more contrasted on a given trial based on four regressors: a constant intercept reflecting the subject’s individual preference for (or against) reporting the left side, single-trial prestimulus \( \alpha \) amplitudes, single-trial contrast differences between left and right stimulus, and the interaction between amplitude and contrast differences. This model was applied independently for each participant, channel, and time point.

**Figure 3.** Similarity between cue-induced and spontaneous lateralization, in the comparison between high and low perceptual uncertainty. **A**. The definition of trials with high uncertainty was performed by selecting a range of \( \pm 0.25 \) around the PSE, defined as the point where the probability of response for either of the hemifields is 0.5. This resulted, across all participants, in two distinct sets of trials (color-coded distributions in right inset). **B**. Similarity matrix between the cue-induced and the spontaneous lateralization, in the comparison between high and low perceptual uncertainty as defined in A. The comparison yields a significant cluster of similarity at \(-200\) ms prestimulus, indicating that the pattern of spontaneous lateralization is more congruent to the one induced by the cue when there is higher perceptual uncertainty.
objective contrast differences, thereby confirming the results of our previous analyses. To further illustrate how this biasing effect plays out for different objective contrast differences, we grouped trials into five bins according to their contrast difference. Then for each subject, we selected the channel with the highest \( \beta \) score, indicating that strong \( \alpha \) amplitude at this channel was most predictive for a leftward response, and the channel with the lowest \( \beta \) score. We then inverted the model to compute the probability of a leftward response for each of the five contrast bins, separately for trials with strong or weak amplitude at each of the two channels of interest. We then computed for each contrast bin and each channel the difference in probability for a leftward response on strong minus weak amplitude trials, and in turn subtracted this difference at the channel with highest \( \beta \) score from the channel with lowest \( \beta \) score. Thus, the result of this double subtraction indicates which objective contrast differences were most affected by the biasing effect of prestimulus \( \alpha \) amplitude. As shown in Figure 4B, this effect was strongest for the central contrast bin comprising contrast differences around the PSE (i.e., trials with highest perceptual uncertainty).

Figure 4B shows topographies indicating for each channel the interaction between prestimulus amplitude and objective contrast difference on the probability of a leftward response, illustrating a significant, nonlateralized negative cluster (cluster...
We did not find any variation in the strength and directionality across subjects variability in the general preference to report either hemifield. At the same time, we also observed strong across-subjects variability in the general preference to report either hemifield. Indeed, we found a significant cluster (Fig. 5A, cluster \( p = 0.006, \text{two-tailed}, \text{cluster } r = 0.355 \)) spanning a great portion of the prestimulus window. The highest peak of the correlation, at \(-379 \text{ ms before stimulus} (r = 0.391, p = 0.006)\) is shown in Figure 5B.

This result demonstrates that participants with an overall preference to report the left stimulus as more contrasted also showed a congruent lateralization pattern in the difference between left versus right responses, and vice versa, suggesting that the large interindividual variability in subjective contrast perception is partially rooted in the same patterns of cortical prestimulus excitation and inhibition that also bias trial-by-trial decision-making.

**Discussion**

Do spontaneous fluctuations in \( \alpha \) amplitude alter perceived contrast? To answer this question, we used a contrast discrimination task in which two Gabor patches were presented in the left and right hemifield, and participants reported the stimulus with the highest contrast (Carrasco, 2011). Based on the finding that strong \( \alpha \) amplitude is associated with reduced cortical excitability (Bollimunta et al., 2008; Romei et al., 2008; Haegens et al., 2011), we expected that perceived contrast of the stimulus represented in the more excitable cortical hemisphere would be amplified. Across several analyses, we confirmed this relationship between contrast appearance and prestimulus \( \alpha \) amplitude lateralization just before stimulus onset. Specifically, stimuli contralateral to...
the hemisphere with weaker prestimulus $\alpha$ amplitude were more likely to be reported as more contrasted (Figs. 2B,C, 4).

**Spontaneous $\alpha$ lateralization biases subjective appearance**

Numerous studies have demonstrated that the amplitude of alpha band oscillations is not only related to physiological excitability, but also to behavioral performance (Ergenoglu et al., 2004; Van Dijk et al., 2008): in detection tasks, weak $\alpha$ amplitude, indicating increased cortical excitability, is associated with a more liberal detection criterion (Iemi et al., 2017; Iemi and Busch, 2018), higher confidence (Samaha et al., 2017), and higher subjective stimulus visibility (Benwell et al., 2017), but without a change in accuracy. At present, it is still debated whether these effects indicate a change at the level of subjective perception of the visual world, or a change in observers’ strategic decision-making, whereby weak alpha power induces a preference to report “yes, there was a target” without inducing a change in the percept (Kloosterman et al., 2019; Samaha et al., 2020a). This debate has been hard to resolve given that previous studies have not actually required participants to make judgments about stimulus appearance (e.g., contrast) and have instead inferred effects on appearance from effects on hit rates. However, as illustrated by the phenomenon of blindsight, detection, and subjective appearance can strongly dissociate, implying that they are not identical phenomena.

Our work significantly advances the existing literature by asking the participants to judge stimulus contrast directly, eliminating any need to infer appearance from detection hit rates. Furthermore, the comparative nature of the task eliminates any potential role of the kind of strategic decision bias described above. In simple words, an increased strategic preference to report “yes, there was a target” cannot affect performance in a task that does not ask for target-presence. In this sense, the comparative contrast judgment also has an advantage over combining single-interval target detection with introspective visual awareness ratings. Although suggestive, an association of alpha power and higher awareness ratings (“I experienced the target clearly”) could still be interpreted as a strategic preference for higher ratings rather than a genuine change in subjective perception. To summarize, using an adaptation of the paradigm originally proposed by Carrasco et al. (2004) allowed us to show strong evidence for an effect of prestimulus alpha band oscillations on subjective perception while avoiding fundamental ambiguities in previous studies on the role of prestimulus oscillations in perception. The ability of the Carrasco paradigm to distinguish an effect of attentional cueing on subjective appearance versus strategic bias has been disputed (Schneider and Komlos, 2008; Schneider, 2011; Schneider and Malik, 2021). The core of this critique is that observers are undoubtedly aware of the salient attentional cue, which in turn may change their strategic preference to report the cued location as having stronger contrast. While Carrasco and colleagues have provided several counterarguments against this criticism (Anton-Erxleben et al., 2010, 2011; Carrasco and Barbot, 2019), we would like to point out that our adaptation of their paradigm is not vulnerable to the same criticism to begin with. Specifically, our study did not assess the perceptual effect of an exogenous cue, but of endogenous, prestimulus amplitude lateralization. A central finding was that the prestimulus effect was restricted to the moment just before stimulus onset. While it is reasonable to assume that observers are aware of cues, there is no published evidence to suggest that they are aware of the momentary state of their $\alpha$ lateralization, or that they are able to manipulate their lateralization with this degree of temporal precision.

What gave rise to these spontaneous shifts of excitability in the first place? Voluntary spatial cues induce an $\alpha$ amplitude decrement in the contralateral relative to the ipsilateral hemisphere, indicating greater excitability in the task-relevant hemisphere and greater inhibition in the task-irrelevant hemisphere (Sauseng et al., 2005; Thut et al., 2006; Foxe and Snyder, 2011) and such lateralization can also occur spontaneously in the absence of external cues, driven only by internal fluctuations in the deployment of spatial attention (Bengson et al., 2014; Boncompte et al., 2016). Moreover, we compared the spontaneous prestimulus lateralization patterns that predicted participants’ contrast judgments to lateralization patterns induced with conventional spatial cueing and found that these patterns were highly similar (Figs. 2, 3). On the other hand, the cue-induced lateralization shows a different temporal profile and magnitude from the spontaneous lateralization. This difference speaks in favor of two partially dissociable phenomena, whose interrelationship should be addressed in further studies.

**The relationship between idiosyncratic bias and spontaneous lateralization**

In addition to this within-subjects relationship between prestimulus alpha band lateralization and contrast judgments, we found a strong relationship across subjects between individuals’ overall lateralization pattern and their general tendencies to judge one hemifield has having higher contrast (Fig. 5B). Specifically, participants with a general idiosyncratic bias to judge, say, the left stimulus as having higher contrast showed stronger leftward lateralization on trials when the left stimulus was judged as more contrasted, compared with less biased participants. This result suggests that the large interindividual variability in subjective contrast perception is partially rooted in the same patterns of cortical prestimulus excitation and inhibition that also bias trial-by-trial perceptual experience. This finding nicely extends a set of previous research connecting individual biases with prestimulus, spontaneous alpha rhythm (Grabot and Kayser, 2020), by showing that local patterns of $\alpha$ increase and decrease not only influence the decision of participants at the single-trial level, but that participants with different bias direction and strength show differential prestimulus patterns congruent with their own biases. Notably, when the time course of the trial-by-trial effect of lateralization on contrast reports is compared with the time course of the across-subjects correlation, the two patterns show a striking complementarity: indeed, the significance of the correlation across participants fades away exactly when the pattern associated with the trial-by-trial effect ramps up. This complementarity might suggest the presence of two partially independent phenomena. On the one hand a “trait-like” effect, being the idiosyncratic bias, extended throughout the whole prestimulus window. On the other hand, a “state-like” effect, which is associated with the subjective report of contrast on a specific hemifield. Within this framework, such complementarity could be explained as a transition between these two states: the idiosyncratic bias would explain the intersubject variability in spontaneous lateralization in the early prestimulus window. This intersubject variability vanishes in the time window most proximal to the stimulus onset, to leave place to a momentary lateralized state that biases the subjective report, with a consistent pattern across participants. This result is of outstanding interest.
because it suggests one possible mechanism at the basis of the great intersubject variability in perception.

**Nonlateralized α and the quality of sensory representation**

In addition to the effect of prestimulus lateralization on subjective contrast appearance, our regression analysis also showed that stronger bilateral prestimulus α amplitude was associated with reduced objective contrast discrimination accuracy. This result was unexpected because it conflicts with recent studies showing that prestimulus α amplitude affects criterion, not accuracy in visual detection tasks (Limbach and Corballis, 2016; Iemi et al., 2017; Iemi and Busch, 2018), and does not affect performance in discrimination tasks (Benwell et al., 2017; Samaha et al., 2017, 2020b; Benwell et al., 2021). Given that states of high α amplitude indicate low arousal (Johnston et al., 2020), one possibility is that the effect we observed was merely a byproduct of fatigue, which in turn caused the effect on accuracy. However, this interpretation can be ruled out given that accuracy actually improved over time despite the expected increase in nonlateralized occipito-parietal α amplitude. Therefore, the present finding and that of a recent study by Zhou et al. (2021) may indicate that moment-by-moment fluctuations in spontaneous α amplitude can, under some conditions, affect the quality of stimulus representations.

In conclusion, we demonstrate that the amplitude of prestimulus α oscillations alters subjective contrast appearance, such that perceived contrast is amplified for stimuli represented in the cortical hemisphere with weaker amplitude, and thus stronger neuronal excitability. These findings show that spontaneous oscillations affect not only decision-making processes, but can alter our phenomenological perception of the visual world.

**References**


