Prestimulus alpha power is related to the strength of stimulus representation

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Abstract

Spatial attention can modulate behavioural performance and is associated with several electrophysiological markers. In this study, we used multivariate pattern analysis in electrophysiology data to investigate the effects of covert spatial attention on the quality of stimulus processing and underlying mechanisms. Our results show that covert spatial attention led to (i) an anticipatory alpha power desynchronization; (ii) enhanced stimuli identity information. Moreover, we found that alpha power fluctuations in anticipation of the relevant stimuli boosted and prolonged the coding of stimulus identity.

Keywords: spatial attention, alpha oscillations, multivariate pattern analysis, EEG

Introduction

Attention is essential to select and process sensory stimuli in the environment. One of the main difficulties in studying attentional selection in humans is assessing the quality of processing of attended and ignored stimuli. In general, measures such as the amplitude of electrophysiological evoked responses (i.e. N1, P1) have been used as a reflection of this processing. However, a recent study has questioned this view since the amplitude of the evoked response was not correlated with a boost in the target representation.[1]. Moreover, how well the unattended stimulus is processed is particularly hard to assess, given that participants are typically asked not to respond to these events.

One possibility is to use methods which evaluate neural processing without necessarily requiring a behavioural response. Recent studies have relied on multivariate pattern analysis (MVPA) techniques to analyze EEG/MEG responses.[2–4]. In general, these methods are based on the theoretical basis that the MEG/EEG signal reflects coupled dipoles activity of neural circuitry. Although the specific dipole activity may not be identified, their summation would result in different patterns of activity across MEG/EEG sensors[2–4]. These MVPA methods have been increasingly used to understand the effects of attention and its underlying mechanisms. Several studies have shown that spatial attention modulates stimulus representation in working memory[5–7] and sensory information input[8]. Moreover, temporal attention seems to enhance relevant sensory information input, creating a temporal protection window against distractors[1], and boosting its representational content.

Another pre-activating mechanism commonly described in the literature of spatial attention is the modulations in the spectral characteristics of the alpha (8-16 Hz) band[9]. This oscillatory activity is associated with cognitive functions such as visual attention[10], working memory[11] and cognitive load[12]. For example, anticipatory lateralized desynchronisation of alpha power is correlated with spatial expectations of a relevant upcoming stimuli in a particular hemifield[10,13]. Studies suggest that alpha oscillations can play a role in information processing by suppressing the activity of particular neural populations involved with the irrelevant stimuli feature/field processing, and by selecting the inhibition release of task-related neural populations[14,15]. Therefore, activity of alpha oscillations is also a potential mechanism in preparing the neural system to enhance relevant signal processing in anticipation to expected events. Nevertheless, recent

studies have challenged the view of ongoing alpha oscillations affecting perceptual precision, but rather affecting perceptual[16] or decision bias[17,18].

In the present work, we combined both analyses to investigate: (1) how covert spatial attention modulates stimulus representation; (2) whether and how different EEG markers are modulated. To do so, a stream of stimuli was presented at the right and left side of a screen and participants had to perform an oddball task at the relevant side while EEG was recorded. Multivariate pattern analyses were performed to investigate the effect of covert spatial attention during stimulus processing. We compared whether the classification scores of ignored and attended stimuli were better than at chance and whether they differed. Moreover, we measured whether decoding strength was correlated with potential oscillatory mechanisms such as alpha desynchronisation.

Materials & Methods

Participants

Twenty participants (age range, 18-27 years; 11 female) gave informed consent to participate in this study. Data from one participant was excluded from the final analysis due to excessive noise in the EEG signal. All participants had normal or corrected-to-normal vision and were free from psychological or neurological diseases. The experimental protocol was approved by the Research Ethics Committee of the Federal University of ABC.

Apparatus

Stimuli were presented using the Psychtoolbox v.3.0 package for MATLAB on a 20-inch CRT monitor with a vertical refresh rate of 60 Hz, placed 50 cm in front of the participant. EEG was recorded continuously from 64 ActiCap Electrodes (Brain Products) at 1000 Hz by a QuickAmp amplifier (BrainProducts). All sites were referenced to FCz and grounded to AFz. The electrodes were positioned according to the International 10-10 system. Additional bipolar electrodes registered the electrooculogram (EOG).

Procedure

Each block began with the presentation of a central fixation point (white, 0.4°) and two circles (horizontal eccentricity of 5°, size of 3°), one at the left and the other at the right side of the fixation point (Figure

1A). Each experimental block consisted of two streams of stimuli, presented inside the circles in one of the visual hemifields. Stimuli presentation was one at a time, alternating between visual hemifields, always starting at the left side, with an SOA of 500 ms between them (2Hz frequency). Participants had to identify the oddball stimuli within a stream of standard stimuli presented at a specific side by pressing a button with their right index finger. Standard visual stimuli were vertical/horizontal oriented Gabor patches (3 degrees of visual angle) with a spatial frequency of 2 cycles per degree (cpd). The oddball stimuli (target) were vertical/horizontal oriented Gabor patches (3°) with a higher spatial frequency defined by an adaptive procedure. There were 70% of standards (half vertical and half horizontal) and 30% of targets. All stimuli lasted 0.1 s.

Each block was preceded with an instruction screen indicating in which visual hemifield (right or left) the participant had to detect targets, thus resulting in two main experimental situations: attend to the right or left hemifield. Volunteers were instructed to fixate at the fixation point, but also to allocate their covert attention to the indicated side. Each block consisted of 120 stimuli, 60 for each location, with 18 targets. There were 36 blocks (18 blocks for each condition). Block types were presented in a pseudorandom order (not more than three same attended side blocks in a row).

The session began with volunteers performing a training session, which consisted of one block of the experimental procedure followed by a weighted up-down staircase procedure[19]. The staircase block was shorter, with 80 stimuli. After every 12 attended side stimuli presentation, the spatial frequency value was recalculated based on accuracy. A psychometric function was fitted to the data to obtain the spatial frequency corresponding to 75% of correct responses.

EEG pre-processing

EEG pre-processing was carried out using BrainVision Analyzer (Brain Products). All data were down-sampled to 250 Hz and re-referenced to ear electrodes. For eye movement artifact rejection, an independent component analysis (ICA) was performed on filtered (Butterworth Zero Phase Filter between 1 Hz to 30 Hz) data. Eye related components were identified by comparing individual ICA components with EOG channels and by visual inspection.

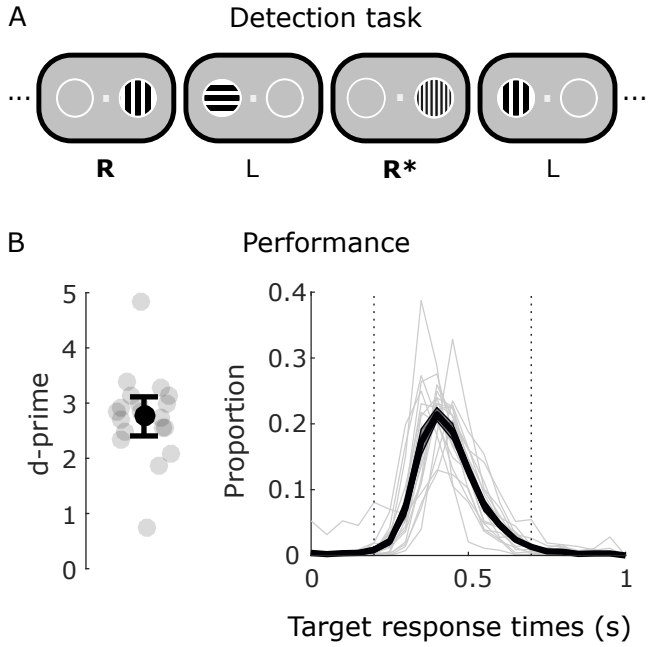

Figure 1. A) Each experimental block began with the presentation of a fixation point. Visual stimuli appeared in sequence, in alternated sides, separated by an interval of 0.5 s. In different blocks, participants had to respond to the oddball target either on the right or left stream. The oddball stimuli (target) were Gabor patches with a higher spatial frequency defined by a staircase procedure. There were 70% of standards and 30% of targets. All stimuli lasted 0.1 s. B) Left: Distribution of participants' d-primes (circles) and its respective errorbar (mean, S.E.M). Right: Reaction times for targets (mean, S.E.M). Dashed lines represent the interval that was considered as hits. Lighter lines represent individual response times.

EEG analysis

EEG analyses were based only on standard stimuli to avoid contamination from motor responses. Standard stimuli presented 500 ms before or 200 ms after a motor action were also excluded from further analyses. Stimuli were separated, in different analyses, based on Attention (attended/ignored), stimuli hemifield occurrence (right/left), and stimuli orientation (vertical/horizontal).

ERP consisted of a filtered (Butterworth Zero Phase Filter between 0.05 Hz to 30 Hz) segmented (-0.25 to 0.495 s, where 0 is the onset of the stimulus) and baselined (-0.25 to 0 s) data. For the frequency analysis, no-filters were used and data were segmented between -1.95 and 1.95 s relative to stimulus onset. Time-frequency analysis was based on a short-time Fourier transform of Hanning tapered data. We estimated frequencies between 4 and 40 Hz, using a frequency dependent time window of 5 wavelengths that was advanced over the data in 20-ms steps. Power was logarithmically transformed in the end.

For the MVPA analysis, ERP data from all conditions and all electrodes were exported from MATLAB to

Python 3 Jupyter Notebook (5.0.0) to decode stimulus orientation by using Scikit-learn library. For the main experiment analysis, classification of grating orientation (vertical or horizontal) was performed separately for each attention condition and side (attended stimulus presented at the left hemifield, ignored stimulus at the left hemifield, attended stimulus at the right hemifield, ignored stimulus at the right hemifield). All channels were used as features for the classification procedure. The classification pipeline consisted of a leave-one-block-out cross-validation (18 blocks) procedure. Training and test data were normalised between 0 and 1 based on the training data, and a logistic classifier with a l2 regularisation was used with all parameters set to the default in Scikit. For each participant, time point and model, the logistic regression pipeline returned labels' probabilities of the trials and the area under the receiver operating characteristic curve (AUC) was calculated as performance score. Afterwards, left and right models were averaged with respect to attended and ignored conditions.

Statistics

Relation between reaction times and pre-stimulus alpha power

We ran two generalised linear mixed-effects models in MATLAB (glme), a linear model using log-transformed reaction times as the dependent variable and a second binomial one considering hits as the dependent variable. Pre-stimulus alpha power was the fixed factor, and participants' slope and intercept in alpha power were the random factors.

EEG

Cluster-based paired t-test was performed by calculating permutation tests in which attended and ignored conditions were intermixed within each participant in 1000 random permutations[20]. Such statistical analyses were performed for the ERP, time-frequency and Fourier Transform analysis in MATLAB. Moreover, cluster-based analysis with 1000 permutations as implemented in the MNE library[21] was performed to calculate whether models' decoding scores were statistically different from the null-hypothesis (AUC = 0.5, function: *permutation_cluster_1samp_test*, threshold = 2.5), and to calculate whether attended and ignored conditions had different distributions of decoding scores (function: *permutation_cluster_test*, threshold = 2.5).

Results

Behavioural results

Participants' performance were computed considering hits as responses between 200 ms to 700 ms after a target was presented at the attended side (Figure 1B, right). All other responses were considered false alarms. Participants were able to perform the detection task (Hit Rate: mean = 0.74, std = 0.15, min = 0.34, max = 0.98; and d': mean = 2.66, std = 0.84, min = 0.71, max = 4.82, Figure 1B, left).

Event related potentials

To investigate the effects of attention on event-related potentials, we focused on contralateral electrodes relative to the visual hemifield of the standards stimuli. Specifically, we focused on parieto-occipital electrodes (Right hemifield conditions: PO9/PO7/ PO3/O1; Left hemifield conditions: PO10/PO8/PO4/O2), baselined between -50 to 50 ms. Although attended stimuli evoked a stronger negative peak around 180 ms (Figure 2, left), there was no significant difference between attended and ignored conditions (highest negative cluster-stat = 51.3833, p = 0.18, time = 0.172 to 0.2, highest positive cluster-stat = 51.3833, p = 0.068, time = 0.42 to 0.5). Although we did not find significant differences between conditions, it is important to notice it is hard to disentangle attended and ignored ERP due to the fixed SOA design and possible component overlapping. However, there was clear activity lateralization due to attention (Figure 2, right).

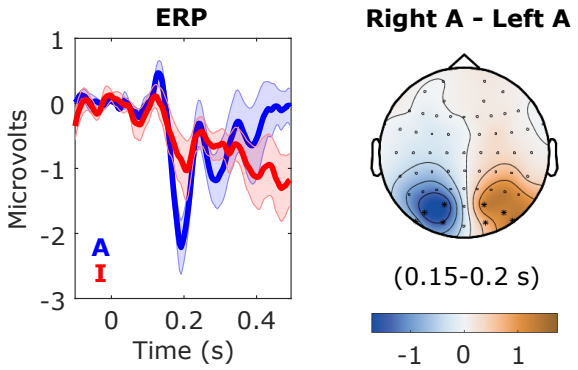

Figure 2. Event related potentials. Left: Activity evoked by attended (blue) and ignored (red) standards. Time point zero corresponds to the onset of stimuli. Right: Topoplot showing the difference between the average of the attended stimuli activity at right and left hemifields from 150 ms to 200 ms.

Alpha-band oscillations

Alpha band desynchronization is a key marker of attention. Therefore, we compared the power spectrum of attended and ignored conditions. Similar to the ERP analysis, we focused on the same parieto-occipital contralateral electrodes to stimulus presentation when that stream was to be attended or ignored(Figure 3A). There was a difference in power evoked by attended and ignored stimuli (positive cluster-stats = 1203.6, 1269.2, 1791.6, all $p<0.01$; negative cluster-stats = 774.26, $p<0.004$; stats = 502.33, $p = 0.027$). The clusters' period coincides with stimuli occurrence. There was a significant alpha (9 - 15 Hz) power attenuation when attended standard stimuli were about to be presented compared to ignored ones. Our results are consistent with alpha power desynchronization as an anticipatory marker of attention[10,14,22].

To evaluate whether prestimulus alpha power was correlated with performance, we ran two separate mixed-models: one investigating how alpha power modulated reaction times to correct target detection and one investigating how alpha power modulated target detection (hit rate) 3B). To calculate the prestimulus alpha power and to avoid activity from the target, we ran a Fast Fourier Transform with a Hanning taper between 8 to 12 Hz on a shorter epoch (-0.3 to 0 s relative to stimulus onset). We did not find a significant effect of alpha power on reaction time (alpha fixed effect: t=0.404, p=0.686), or hit rate (alpha fixed effect: t=-1.76, p=0.078).

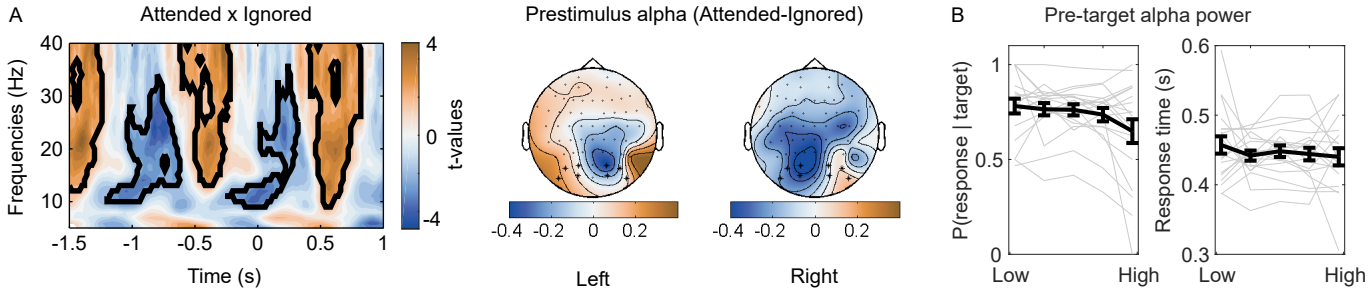

Figure 3. A) Left: Power spectrum paired t-test comparison between attended and ignored stimuli. Black contours indicate significant clusters. Right: Alpha power (dB) topography from the difference between attended and ignored stimuli at a prestimuli time period (-0.5 to 0 s). Asterisks represent used parieto-occiptal channels. B) Error bars (mean, S.E.M) illustrating hits and reaction times for the pre-target alpha power bins. Individual responses for different bins are represented in the background.

Multivariate pattern analyses

We used an l2-regularised logistic regression to test whether orientation information could be decoded in different conditions. We trained and tested separately for each attention and side and, subsequently, we averaged the scores separately for attended and ignored conditions (Figure 4 A). We found that classification was above chance levels for attended stimuli (Attended right: time = 0.184 to 0.224, cluster-stat = 41.351, p = 0.031; Attended left: time = 0.144 to 0.18 and 0.384 to 0.408, cluster-stats = 41.19 and 26.72, p = 0.006 and p = 0.034; Attended [mean], time: 0.148 to 0.224, 0.26 to 0.324, 0.356 to 0.428, cluster-stats = 81.23, 63.11, and 71.11, p = 0.002, 0.002, 0.002). There was no significant clusters in Ignored conditions. A second cluster-based analysis comparing Attended and Ignored scores was performed and showed that attended stimuli had higher classification scores than ignored stimuli (time: 0.144 to 0.22 s, cluster-stat = 211.332, p = 0.018).

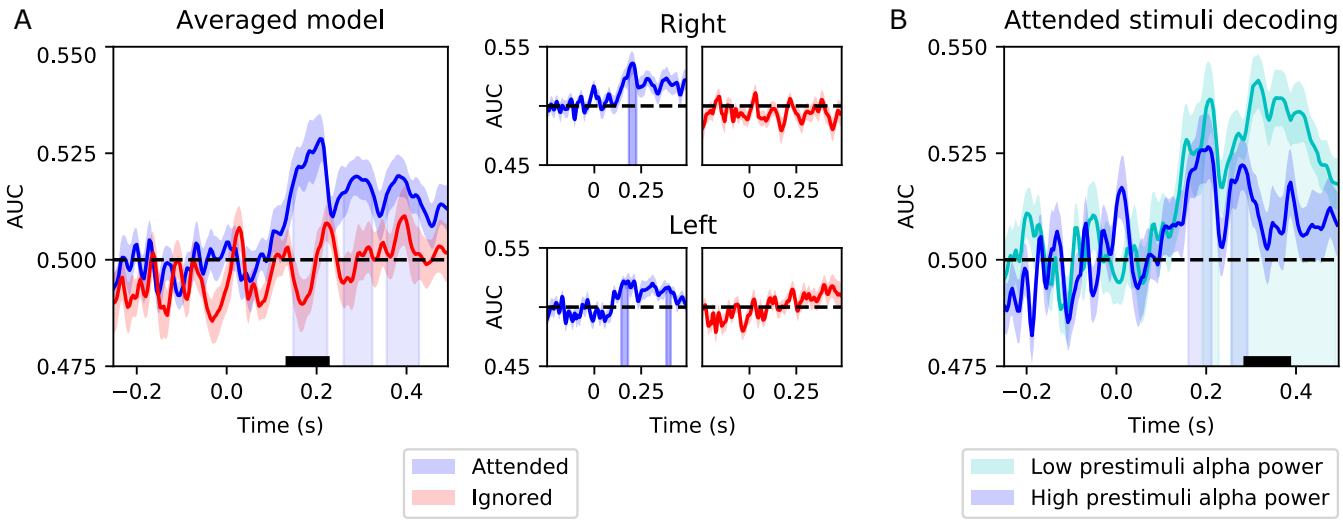

Figure 4. A) Decoding scores across different experimental conditions. Red (ignored) and blue (attended) lines represent mean and error bars represent standard error of the mean. Time zero is the moment in which a standard was presented. Shadows under the curve represent clusters where classification was better than chance. The black line at the left panel shows the cluster period in which classification was higher in attended than in ignored conditions. B) Decoding scores for attended stimuli (mean, S.E.M) grouped into low (cyan) and high (darker blue) prestimuli alpha power. The black line shows the cluster period in which classification was higher in low alpha power trials than in high alpha power trials, and shadows under the curve represent the statistical clusters different from scores at chance.

Given that attention modulated both alpha power and classification accuracy, we tested whether prestimulus alpha desynchronisation was correlated with an increased classification. To test this hypothesis,

we performed a median split on attended stimuli based on their prestimulus alpha power and reran the classification analysis for each group, participant and time point (Figure 4 B). Both low and high prestimulus alpha power groups had decoding scores above chance (Low alpha bin: clusters-stat = 42.40 and 288.461, p = 0.015 and 0.001, time = 0.192 to 0.232 and 0.256 to 0.492; High alpha bin: cluster-stats = 46.998 and 33.841, p = 0.005 and 0.021, time = 0.16 to 0.216 and 0.256 to 0.296). A direct comparison between both conditions showed a higher decoding score for stimuli preceded by low alpha power (cluster-stat = 168.519, p = 0.014, time = 0.296 to 0.38), suggesting that pre-stimulus alpha power was correlated with higher classification scores.

Discussion

In the present study, we investigated the effects of covert spatial attention on sensory information and related mechanisms. Attention resulted in a pre-stimulus alpha desynchronization on contralateral sensors. Using a multivariate decoding approach, we found that spatial attention enhanced target identity coding. Moreover, we found that that stronger alpha desynchronisation boosted the representation of target identity.

Several studies have shown that visual-spatial attention elicits larger P1 and N1 components for attended than for ignored-stimuli[23]. However, P1 and N1 effects seem to indicate distinct attentional mechanisms: while P1 modulation suggests a suppressing mechanism, it has been suggested that N1 modulation represents a sensory gain mechanism[24]. In this study, we did not find a significant effect of attention on event-related potentials. One crucial difference in our study is that events were presented sequentially in a stream. This type of presentation leads to overlaps of event-related potentials which, in turn, might have made it harder to find effects on early components. Moreover, it has been recently suggested that stronger response amplitudes (i.e. ERP, BOLD response) do not necessarily imply enhancement in information about stimulus identity[25]. A recent study investigating temporal attention found a modulation in N1, but no correlation between N1 amplitude and the decoding scores[1]. Therefore, it seems that an increase in signal-noise-ratio is not necessarily linked to boosting information about stimulus identity.

We observed a stronger contralateral alpha decrease in anticipation of attended targets. Our results are in agreement with several studies that have shown that alpha oscillations are correlated with spatial attention[6,26–30]. There has been an increasing discussion as to whether alpha oscillations are associated

with an increase in perceptual processing or if it modulates performance biasing perceptual[16] or decisional mechanisms[17,18]. In recent studies, it has been suggested that decreased alpha power does not improve perceptual acuity, but biases perception by increasing baseline excitability[16–18]. This proposal is based on findings that show that: (1) decreased alpha power was associated with a higher tendency to report the presence of a stimulus, even when a target is absent; (2) alpha power did not affect performance on discrimination tasks[16–18]. In our experiment, the behavioural task was to detect the presence of a target, marked by an increase in the spatial frequency of the Gabor. Although not significant, there was a tendency of higher reportability rates when alpha power decreased, making our results compatible with the perceptual bias proposal.

Our decoding results showed that spatial attention enhanced target identity coding. Even though the decoded feature (stimulus orientation) and the task-relevant feature (spatial frequency) are independent, they share commons mechanisms and attending to one of them seems to affect the other. Within the attended field, decoding was increased in trials with decreased alpha power. Although this finding appears to be more easily explained with the idea of alpha being associated with perceptual precision, it is worth to point out that the increase in decoding was in a later period. This result is consistent with a previous report that found that lower alpha can reduce the immediate interference by a distractor[1]. Given that participants did not make judgements about the orientation of the target, it is not possible, with our current experiment, to be sure whether an increase in decoding would be translated into an increase in the behavioural discrimination.

We conclude that stimulus identity processing is modulated by covert spatial attention and that anticipatory alpha power is associated with such processing.

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