

Alpha/beta power decreases track the fidelity of stimulus-specific information

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Abstract

Massed synchronised neuronal firing is detrimental to information processing. When networks of task-irrelevant neurons fire in unison, they mask the signal generated by task-critical neurons. On a macroscopic level, mass synchronisation of these neurons can contribute to the ubiquitous alpha/beta (8-30Hz) oscillations. Reductions in the amplitude of these oscillations, therefore, may reflect a boost in the processing of high-fidelity information within the cortex. Here, we test this hypothesis. Twenty-one participants completed an associative memory task while undergoing simultaneous EEG-fMRI recordings. Using representational similarity analysis, we quantified the amount of stimulus-specific information represented within the BOLD signal on every trial. When correlating this metric with concurrently-recorded alpha/beta power, we found that as alpha/beta power decreased, our metric of stimulus-specific information increased. We observed this phenomenon during both visual perception and episodic memory retrieval. Further analysis revealed that this effect was better explained by alpha/beta power decreases providing favourable conditions for information processing, rather than directly representing information. Together, these results indicate that alpha/beta power decreases parametrically track the fidelity stimulus-specific information represented within the cortex.

Keywords: neural oscillations; EEG; fMRI; episodic memory; perception

Introduction

Neuronal activity fluctuates rhythmically over time. Often referred to as “neural oscillations”, these rhythmic fluctuations can be observed throughout the brain at frequencies ranging from 0.05Hz to 500Hz (Buzsáki & Draguhn, 2004). When recording from the human scalp, it is the alpha and beta frequencies (8-12Hz; 13-30Hz) that dominate. Alpha/beta activity displays an intimate link to behaviour; engaging in a cognitive task produces a large reduction in the alpha/beta power (amplitude squared). These task-induced power decreases are ubiquitous, and can be observed across, sensory modalities, and cognitive tasks. Given their ubiquity, it stands to reason that these decreases reflect a highly general brain process. While numerous domain-general processes have already been ascribed to alpha/beta oscillations (e.g. idling; Pfurtscheller, Stancák, & Neuper, 1996; inhibition; Jensen & Mazaheri, 2010; Klimesch, Sauseng, & Hanslmayr, 2007), we provide empirical evidence in support of a new perspective: alpha/beta power decreases are a proxy for information processing.

To successfully process information about a stimulus, the brain must be capable of elevating the signal of said stimulus above the noise generated by ongoing neuronal activity (Harris & Thiele, 2011). In situations where the ongoing spiking of a large population of neurons is correlated, this is problematic (Averbeck, Latham, & Pouget, 2006). Mass synchronised spiking generates noise



that conceals the comparatively small neuronal signal evoked by the stimulus, rendering momentary changes in sensory input undetectable (Busch, Dubois, & VanRullen, 2009) and responses to temporally-extended changes unreliable (Goard & Dan, 2009). Reducing these neuronal “noise correlations”, therefore, can boost the signal-to-noise ratio of an evoked neuronal response to a stimulus. Indeed, numerous studies have demonstrated that the decorrelation of task-irrelevant neuronal firing accompanies engagement in cognitive tasks (Churchland et al., 2010; Goard & Dan, 2009; Mitchell, Sundberg, & Reynolds, 2009; Poulet & Petersen, 2008). Given that these noise correlations show a strong positive correlation with the local field potential (LFP) (Cui, Liu, McFarland, Pack, & Butts, 2016), one may speculate that task-related reductions in alpha/beta LFP (Haegens, Nacher, Luna, Romo, & Jensen, 2011) are (to some degree) a marker of the reduction of noise correlations. Such a hypothesis would explain why reductions in alpha/beta power are associated with the successful execution of a wide range of cognitive tasks, from visual perception to memory retrieval.

Here, we test the hypothesis that alpha/beta power decreases are a proxy for information processing. Specifically, we predict that as the amount of stimulus-specific information within the cortex increases, concurrently-recorded measures of alpha/beta power will decrease. Twenty-one participants took part in an associative memory task whilst simultaneous EEG-fMRI recordings were obtained (see figure 1b). On each trial, participants were presented with one of four videos, followed by a noun, and asked to pair the two. Later, participants were presented with the noun and asked to recall the associated video (which would lead to the reinstatement of stimulus-specific information about the video). We first conducted representational similarity analysis (RSA) on the acquired fMRI data to quantify the relative distance between neural patterns of matching and differing videos. This provides a data-driven and objective measure of stimulus-specific information present during a single trial. We then derived alpha/beta power from the concurrently recorded EEG and correlated the observed power with our measure of stimulus-specific information on a trial-by-trial basis. Foreshadowing the results reported below, we found that alpha/beta power decreases negatively correlated with the amount of stimulus-specific information. Importantly, we find evidence for this during both the perception and retrieval of these videos, providing a conceptual replication of our results and supporting the domain-general nature of our hypothesis.

Results

To address our central hypothesis, a single trial measure of stimulus-specific information was computed by comparing the stimulus pattern on a given trial to patterns of matching and differing videos on other trials. For the perceptual data,

this approach involved computing the representational distance for every pair of perceptual trials. These distances were then correlated with a unique model for each trial that stated representational distance for stimuli matching the stimulus presented would be zero and representational distance for stimuli differing from the stimulus presented on this trial would be one. The resulting correlation coefficient was Fisher z-transformed to provide a normally-distributed metric of stimulus-specific information for each trial. Alpha/beta power was calculated and averaged over virtual electrodes, frequency and time. The metric of stimulus-specific information was then correlated with alpha/beta power across trials (see figure 1a). The resulting correlation coefficient was then Fisher z-transformed (to approximate a normal distribution). These Fisher z-values were contrasted against the null hypothesis (there is no correlation; $z = 0$) across participants in a one-sample t-test.

Using this approach, we found a significant negative correlation ($p = 0.044$, Cohen’s $d_z = 0.37$), where a reduction in alpha/beta power was accompanied by an increase in stimulus-specific information (see figure 1b). This result demonstrates that alpha/beta power tracks the fidelity of stimulus-specific information during visual perception.

We then aimed to replicate this effect in the retrieval task, working on the assumption that if alpha/beta power decreases are a proxy for information processing, the phenomenon should generalise across cognitive tasks. The correlation analysis was conducted separately for remembered and forgotten pairs to avoid a spurious correlation driven by memory-related differences in the decreases of alpha/beta power and increases of stimulus-

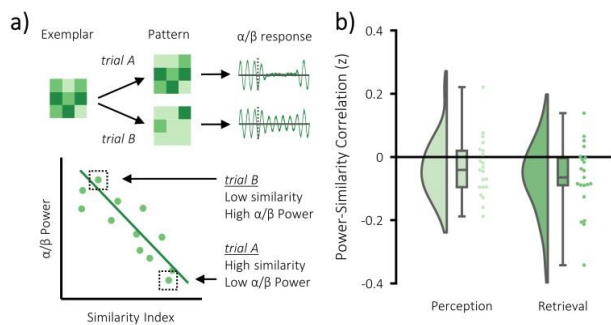


Figure 1. Alpha/beta power decreases track the fidelity of stimulus-specific information. (a) infographic depicting hypotheses and analytical approach. We anticipated that the more a pattern represented matching stimuli relative to differing stimuli, the greater the post-stimulus decrease in alpha/beta power would be. (b) Raincloud plot displaying the correlation between alpha/beta power and stimulus-specific information during visual perception and memory retrieval (each dot represents a single participant; $p < 0.05$. cf. null hypothesis).

specific information for remembered compared to forgotten trials. Representational distance was calculated between each single trial at retrieval and all trials at perception, and then correlated with a model that stated that representational distance for perceived stimuli matching the retrieved stimulus on this trial would be zero and representational distance for perceived stimuli differing from the retrieved stimulus on this trial would be one. The remainder of the analysis is the same as described above.

In line with the previous result, we found a significant negative correlation for remembered trials ($p = 0.004$, Cohen's $d_z = 0.61$), where a reduction in alpha/beta power was accompanied by an increase in stimulus-specific information. No effect was observed when conducting this analysis on forgotten trials ($p = 0.213$, Cohen's $d_z = 0.18$), perhaps because little stimulus-specific information will be represented when the memory cannot be retrieved. These results support the earlier conclusion that alpha/beta power decreases parametrically track the fidelity of stimulus-specific information.

Additional analysis ruled out the possibility that the observed effects (at both perception and retrieval) were driven by trial-by-trial fluctuations in BOLD signal, or retrieval confidence.

Lastly, we asked whether the observed negative correlation between alpha/beta power and stimulus-specific information is better explained by alpha/beta power providing favourable conditions for information representation, or whether alpha/beta power can directly represent information. Here, representational similarity analysis was conducted on the source-reconstructed EEG data in a similar manner to that described for the fMRI data. A Bayesian one-sample t-tests revealed moderate evidence to suggest that alpha/beta power does not represent information during perception ($BF_{10} = 0.230$) or memory retrieval ($BF_{10} = 0.232$).

Discussion

Our central finding demonstrates that as alpha/beta power decreases, the fidelity of stimulus-specific information within the cortex increases. Task-related decreases in alpha/beta power are observable across tasks, sensory modalities, and species. Given their ubiquity, it stands to reason that they reflect a highly general cognitive process. While others have attributed similar results to idling (Pfurtscheller et al., 1996) or inhibition (Jensen & Mazaheri, 2010), we provide evidence that these alpha/beta power decreases are a proxy for information processing. This supports the idea that a reduction of neuronal noise correlations (which map onto local field potential; LFP; Cui et al., 2016) can facilitate the representation of information (Averbeck et al., 2006). Numerous studies have demonstrated that task-irrelevant correlated activity between pairs of neurons is detrimental to stimulus processing (Harris & Thiele, 2011) – particularly for large networks of

correlated neurons (Averbeck et al., 2006) that, incidentally, are more likely to be detected in the LFP. As our conclusion works on the assumption that a reduction in LFP equates to a reduction in noise correlations, we open up an interesting new question: do measures of noise correlations directly map onto an objective and parametric measure of stimulus-specific information? Addressing this question would further strengthen the view that reducing underlying noise can boost the information processing capabilities of the cortex.

Following the hypothesis that alpha/beta power decreases are a proxy for reductions in noise correlations, one would predict that alpha/beta power decreases do not carry representational information about a stimulus. Rather, they provide favourable (i.e. reduced noise) conditions in which another mechanism can allow the internal representation of said stimulus to come forth. In line with this hypothesis, we found moderate evidence to suggest that alpha/beta power decreases do not carry any stimulus-specific information during the perception or retrieval of the visual stimuli. As such, one would view alpha/beta power decreases as a marker for the potential for information processing, rather than directly representing information.

Methods

Thirty-three participants were recruited. All participants were Native English speakers with normal or corrected-to-normal vision. Twelve of these participants were excluded from analysis following technical difficulties and/or poor task performance. Ethical approval was granted by the Research Ethics Committee at the University of Birmingham, complying with the Declaration of Helsinki.

The magnetic resonance imaging data was acquired using a 3T Philips scanner with a 32-channel SENSE receiver coil at the Birmingham University Imaging Centre (BUIC). Functional volumes consisted of 32 axial slices (4mm thickness) with 3x3mm voxels, providing full head coverage (field of view: 192x192x128mm), acquired through an echo-planar imaging (EPI) pulse sequence ($TR=2s$, $TE=40ms$, flip angle of 80°). Eight runs were obtained (4 encoding runs and 4 retrieval runs), each of which acquired 255 volumes plus four dummy scans. A T1-weighted structural image (1x1x1mm voxels; $TR = 7.4ms$; $TE = 3.5ms$; flip angle = 7°, field of view = 256 x 256 x 176mm) was acquired after the second block.

Pre-processing of the fMRI data was conducted in SPM 12. The functional images first underwent slice time correction, followed by spatial realignment to the first volume of each run. The structural T1-weighted image was then co-registered to the mean image of the functional MRI data. The co-registered T1-weighted image was then segmented. For the univariate analysis (see supplementary materials), the functional and structural images were normalised to MNI space, and then smoothed using a

8x8x8mm full-width at half-maximum (FWHM) Gaussian kernel.

The EEG was recorded using a MR compatible Brain Products system (Brain Products, Munich, Germany) and a 64-electrode cap with a custom layout (including an EOG and ECG channel). EEG sampling rate was set to 5 kHz. Impedances were kept below 20 k Ω . All electrode positions, together with the nasion and left and right pre-auricular areas were digitised using a Polhemus Fasttrack system (Polhemus, Colchester, VT) for use in the creation of headmodels for source localisation.

Gradient and BCG correction was run first using the *fmrib* toolbox. All subsequent EEG pre-processing was conducted using the Fieldtrip toolbox. The data was epoched, components relating to eyeblinks were removed, the signal was low-pass filtered, and any residual artifacts were identified and removed through visual inspection. The preprocessed data was reconstructed in source space using individual head models, structural (T1-weighted) MRI scans and 4-layer boundary element models (BEM). The timelocked EEG data was reconstructed using a Linearly Constrained Minimum Variance (LCMV) beamformer.

For time-frequency analysis, first, the source-reconstructed EEG data was convolved with a 6-cycle wavelet (-1 to 3 seconds, in steps of 25ms; 8 to 30Hz; in steps of 0.5Hz). Second, the resulting data was z-transformed using the mean and standard deviation of power across time and trials. Third, the data was restricted to two time/frequency windows of interest (-1000-0ms and 500-1500ms post-stimulus; both 8-30Hz) and then averaged across these windows, resulting in two alpha/beta power values per trial for each virtual electrode.

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